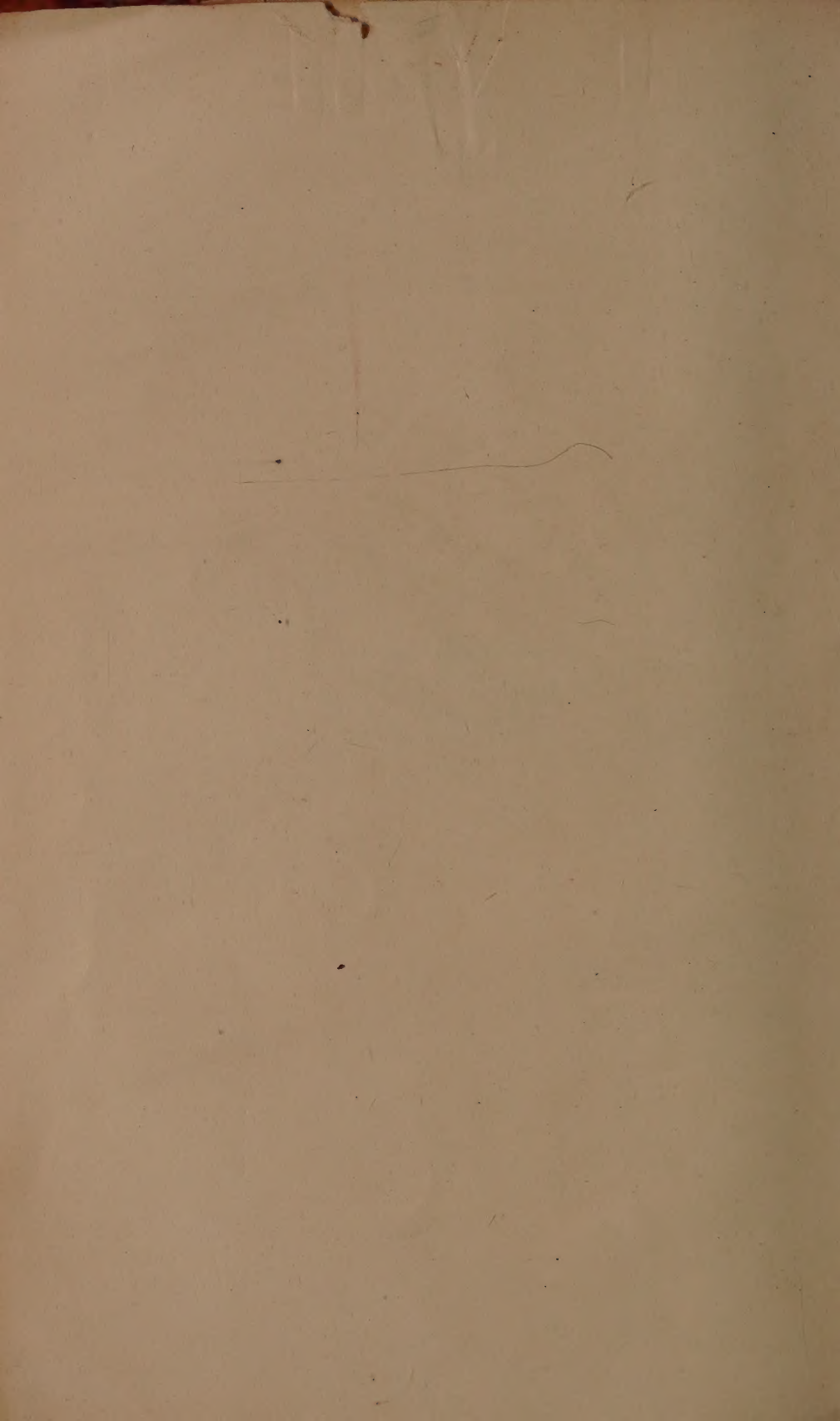


COMM. INST. ENTOM
— LIBRARY —

No. 9397/1

ms.



THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

VOL. 97

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

1946

PRINTED IN GREAT BRITAIN BY
RICHARD CLAY AND COMPANY, LTD.,
BUNGAY, SUFFOLK.

CONTENTS

	PAGE
ASHBY, D. G., M.A., and WRIGHT, D. W., M.A. The immature stages of the carrot fly	355
BEALL, Geoffrey. Seasonal variation in sex proportion and wing length in the migrant butterfly, <i>Danaus plexippus</i> L. (Lep. DANAIIDAE)	337
CHEN, Sicien H. Evolution of the insect larva	381
COLLIN, J. E. The British genera and species of OSCINELLINAE (Diptera, CHLOROPIDAE)	117
CROWSON, R. A., B.Sc., A.R.C.S., D.I.C., F.R.E.S. A revision of the genera of the Chrysomelid group SAGRINAE (Coleoptera)	75
DUFFY, Evelyn A. J., F.R.E.S. A contribution towards the biology of <i>Prionus coriarius</i> L. (Coleoptera, CERAMBYCIDAE)	419
EVANS, J. W., M.A., D.Sc. A natural classification of leaf-hoppers (Homoptera, JASSOIDEA). Part 2: AETALIONIDAE, HYLICIDAE, EURYMELIDAE	39
FRASER, Lt.-Col. F. C., I.M.S. Retd., F.R.E.S. Notes on Amazonian Odonata in the Leeds Museum	443
GARDNER, J. C. M. On larvae of the NOCTUIDAE (Lepidoptera)—II	237
GELSKES, D. C. Observations on the Odonata of Tobago, B.W.I.	213
HALL, W. J., D.Sc., F.R.E.S. New or little known species of DIASPIDIDAE (Coccoidea) from Africa	55
HALL, W. J., D.Sc., F.R.E.S. On the Ethiopian Diaspidini (Coccoidea)	497
HICKIN, N. E., Ph.D., F.R.E.S. Larvae of the British Trichoptera	187
HINTON, H. E., B.Sc., Ph.D., F.R.E.S. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera	1
HINTON, H. E., B.Sc., Ph.D., F.R.E.S. The "gin-traps" of some beetle pupae; a protective device which appears to be unknown	473
RICHARDS, O. W., M.A., D.Sc., and WALOFF, N. The study of a population of <i>Ephestia elutella</i> Hübner (Lep., PHYCITIDAE) living on bulk grain	253
SOMEREN, E. C. C. van. Ethiopian CULICIDAE. Tribe Megarhinini—notes and descriptions	177
TSAI, P. H., and TANG, C. The classification of the Chinese gall Aphids with descriptions of three new genera and six new species from Meitan, Kweichow	405
WALOFF, N., and RICHARDS, O. W., M.A., D.Sc. Observations on the behaviour of <i>Ephestia elutella</i> Hübner (Lep., PHYCITIDAE) breeding on bulk grain	299
ZAKHVATKIN, A. A., D.Sc. Studies on the Homoptera of Turkey	149
GENERAL INDEX	584

Vol. 97. Part 1. Pp. 1-37, 24 figs.

22nd July, 1946.

IMP. INST. ENT.
LIBRARY

13 AUG 1946

SERIAL
SEPARATE

Ent. 344

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

- X HINTON, H. E., B.Sc., Ph.D., F.R.E.S. On the
homology and nomenclature of the setae of
lepidopterous larvae, with some notes on the
phylogeny of the Lepidoptera . . . 1-37, 24 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 12s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.
C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.
H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,
D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Registrar :

Finance and House Committee.

G. FOX-WILSON, N.D.H. (Chairman).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (Chairman).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (Chairman).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (Secretary).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (Chairman).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. **British National Committee for Biology** (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. **Local Committee of Management of Wicken Fen.**

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. **National Trust for Places of Historic Interest or Natural Beauty.**

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. **New Forest Association.**

Mr. W. Fassnidge, appointed 1934.

5. **New Forest Joint Committee.**

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. **Royal Meteorological Society. Phenological Committee.**

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. **Biology War Committee.**

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. **Council for the Promotion of Field Studies.**

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. **Joint Bioclimatic Committee.**

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF LONDON

Vol. 97.

1946.

ON THE HOMOLGY AND NOMENCLATURE OF THE SETAE OF LEPIDOPTEROUS LARVAE, WITH SOME NOTES ON THE PHYLOGENY OF THE LEPIDOPTERA

By H. E. HINTON, B.Sc., Ph.D., F.R.E.S.

(*Department of Entomology, British Museum (Natural History).*)

Manuscript received 1st October, 1945.

(Read 16th January, 1946.)

WITH 24 TEXT-FIGURES.

CONTENTS.

	PAGE
Introduction	1
Cranial setae	5
Thoracic and abdominal setae	14
A. The microscopic or proprioceptor setae	15
B. The long or tactile setae	24
Acknowledgments	35
References	36

INTRODUCTION.

THIS paper owes its origin to certain difficulties I encountered when preparing a monograph of the immature stages of the family TINAEIDAE. While I was describing the larvae of the TINAEIDAE, it became obvious to me that the generally accepted views on the homotypy of many of the setae were wrong. This naturally led me to investigate homologous setae in other families, and I soon found that it was not difficult to disprove some of the homologies established by previous authors. Another reason for making a general survey of the chaetotaxy was the frequent difficulty of discovering from the TINAEIDAE themselves what number and what arrangement of the setae could safely be considered to be primitive or ancestral and what could reasonably be regarded

as specialised. Without this information it was impossible to draw satisfactory conclusions as to the main evolutionary trends within the family; and, as one result of searching for this kind of information, I have tried to distinguish between the primitive and specialised features exhibited by most of the setal groups. I have said nothing of the setae of the tenth abdominal segment for two reasons: in the first place I have been unable to resolve the homotypy of all the setae, though their homologies are clear enough; and, in the second place, the distribution of setae on this segment appears to be of relatively little taxonomic value.

In order to make clear many of my conclusions regarding the primitive and specialised characters of the various setal groups, I am forced to anticipate some of the results of two papers now in preparation, one on the systematic position of the MICROPTERYGIDAE and one on the natural groups within the Lepidoptera. My opinions on these two subjects and many of the reasons for them are shown in fig. 1, which may represent a new method of illustrating phylogenetic concepts. The vertical lines are drawn through what appear to be the maximum and minimum times for the origins of the different groups; and in each case the probable error is considerably greater at the lower than at the upper end. The dates of the periods are taken from Zeuner (1946), who has given a number of reasons for believing that the Tertiary is considerably longer than it is often thought to be. At first sight it may seem strange to place the origin of the Ditrysia in the lower Cretaceous, as no fossil Lepidoptera are known below the Eocene. But this is done, among other reasons that will be discussed in a later paper on this subject, because the most primitive families of the Ditrysia are carnivorous, fungivorous, or lichen feeders, and their feeding habits show no signs of having been fixed at a time when flowering plants were in existence.

The family MICROPTERYGIDAE was first given ordinal rank by Chapman (1917), and for it he erected the order Zeugloptera. This order is accepted here though not for the reasons given by Chapman. Tillyard (1919, 1923a, 1923b) again included the family in the Lepidoptera, agreeing neither with Chapman nor with Comstock, who included the family in the Trichoptera. My objections to Tillyard's arguments will be published in full at a later date, but meanwhile I have given in fig. 1 sufficient reason, I think, to show beyond reasonable doubt that the Zeugloptera are a much more archaic order than either the Trichoptera or Lepidoptera. If the MICROPTERYGIDAE are included in the Lepidoptera, the Trichoptera must be included in the same order.

The Lepidoptera are now divided into two suborders: the Jugatae and Frenatae of Comstock and others and the Homoneura and Heteroneura of Tillyard, Imms, and many recent authors. Some authors still divide the order into Heterocera and Rhopalocera, which is absurd. There are many groups of families of comparable taxonomic rank to the Rhopalocera, so that if the series of families now included in the Rhopalocera is given subordinal rank, many new suborders would have to be erected. The division of the order as proposed by both Comstock and Tillyard has the defect of associating the HEPIALIDAE with the very different ERIOCRANIIDAE in one suborder and placing the INCURVARIIDAE, ADELIDAE, etc., which are far nearer to the HEPIALIDAE as regards the majority of characters of all stages, in another suborder. The division of the Lepidoptera into Jugatae and Frenatae has, among other defects, the curious result of placing the females of some of the more primitive NEPTICULIDAE in the Jugatae and their males in the Frenatae.

The system of classification proposed here more closely resembles that of

Börner (1939) than any other that has been published. The suborder Ditrysia is used by me in exactly the same sense, but I have been forced to divide his Monotrysia into two suborders. I retain the name Monotrysia for the Hepaloidea,

LEPIDOPTERA

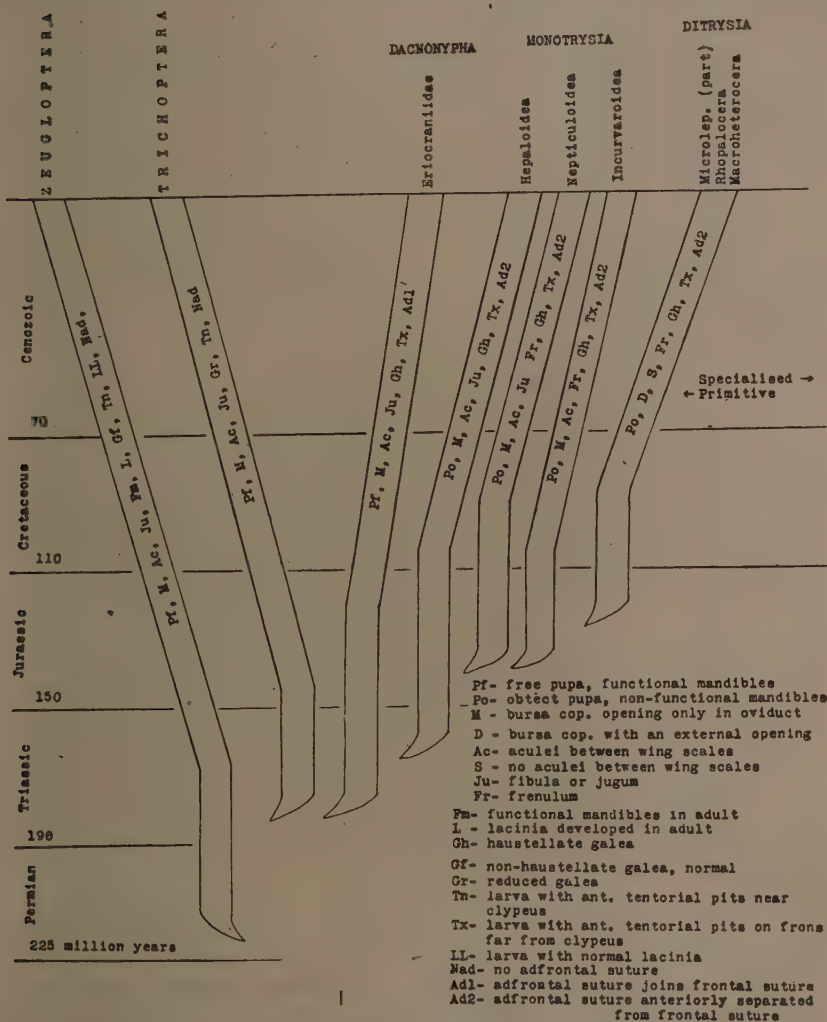


FIG. 1.—Phylogenetic diagram illustrating the relation between the Lepidoptera, Trichoptera, and Zeugloptera and the relation to each other of the three suborders of the Lepidoptera.

Nepticuloidea, and Incurvarioidea, but for the ERIOCRANIDAE and MNESARCHAEIDAE I propose the new suborder Daconypha. The MICROPTERYGIDAE were included in the Monotrysia by Börner (1939).

A brief outline of my system of classification is as follows :—

I. Suborder : **DACNONYPHA** new suborder.

Larva without thoracic legs or abdominal prolegs. Head with adfrontal suture¹ joining anterior margin behind antenna and some distance lateral to frontal suture so that seta A1 is included in the adfrontal sclerite. *Pupa* free and with functional mandibles. *Adult* with venation of fore- and hind-wing very similar; subcosta and main stem of radius separate, the latter forked or simple; radial sector with three or four branches. Aculei present between scales over general surface of wings. Wings coupled by means of a fibula. Head with lateral ocelli. Mandibles absent, or present as untoothed, non-functional lobes; maxilla with palp 5- or 3-segmented; lacinia absent; galea haustellate. Female without a separate external opening to the bursa copulatrix.

The New Zealand MNESARCHAEIDAE are included here with the ERIOCRANIIDAE. Nothing is known of the larva or pupa of the MNESARCHAEIDAE. The Daconypha correspond to Packard's (1895) superfamily Paleolepidoptera of the suborder Lepidoptera—Haustellata.

II. Suborder : **MONOTRYSLA** (Börner, 1939).

Larva without thoracic legs or abdominal prolegs or with both; if prolegs are present, they are always absent on the tenth segment except (HEPIALIDAE) when the frontal puncture of the head is lateral to the frontal seta. Head frequently with two G setae; adfrontal suture joining frontal suture near anterior margin. *Pupa* of an incomplete obtect type with the seventh segment of the male movable except in the HEPIALIDAE (all?); abdomen with series of caudally directed spines on at least some segments; pupa always extruding from cocoon or cell on emergence of adult. *Adult* with venation of fore- and hind-wing very similar or heteroneurus; if similar (HEPIALIDAE) both subcosta and main stem of radius are separate and both are forked or simple, and the radial sector has four branches. Aculei present between scales over general surface of wings. Wings coupled by means of a fibula, or jugum, or frenulum, or both fibula and frenulum. Head without (all?) lateral ocelli. Mandibles entirely reduced; maxilla with palp long and 5-segmented or reduced; lacinia absent (vestigial in HEPIALIDAE according to Börner); galea haustellate though sometimes very short. Female without a separate external opening to the bursa copulatrix.

Division Homoneura : Hepaloidea.

Division Heteroneura : Nepticuloidea, Incurvaroidea.

III. Suborder : **DITRYSLA** (Börner, 1939).

Larva nearly always with thoracic legs and two or more pairs of prolegs, rarely without legs or prolegs, e.g. some GRACILARIIDAE; when legs and prolegs are present, prolegs are always present on the tenth segment and the frontal puncture is always mesal to the frontal seta. Head never with two G setae; adfrontal suture joining frontal suture near anterior margin. *Pupa* of an incomplete or complete obtect type. In lower forms with seventh segment of male movable and with caudally directed series of spines on at least some abdominal segments; pupa always protruding from cocoon or cell on emergence of

¹ Snodgrass (1928, 1935) calls the secondary adfrontal suture the frontal suture, which makes it evident that he has not studied the ontogeny of the head of a caterpillar. The sclerite he calls the clypeus is in fact the frons plus the clypeus, and his frons is only a mesal part of the cranium cut off from the remaining more lateral cranial areas in third or fourth instar larvae when the adfrontal sutures appear for the first time.

adult. In higher forms with seventh segment of male fused to eighth and sometimes with all segments immovable; pupa without caudally directed series of spines on abdomen and rarely protruding from cocoon on emergence of adult. *Adult* with venation of fore- and hind-wings very different; hind-wing with the subcosta and the main stem of the radius fused distally into a single vein, and radial sector simple. Aculei absent or, if present, restricted to certain definite patches on wings. Wings without a fibula or jugum; in lower forms always coupled by a frenulum. Head with or without lateral ocelli. Mandibles absent; maxilla with palp 5-segmented or reduced, sometimes absent; lacinia absent; galea haustellate and nearly always long. Female with a bursa copulatrix which has an external opening as well as one into the common oviduct.

CRANIAL SETAE.

There may be two kinds of setae and punctures on the head, viz.: primary setae and punctures and secondary setae and punctures. Primary setae and punctures are those which are present in the first instar larvae of all groups from the lowest (ERIOCRANIIDAE) to the most specialised such as the SPHINGIDAE. In the *Dacnonypha*, *Monotrysis*, and the more primitive of the *Ditryisia* no additional setae or punctures appear to be gained at succeeding moults, so that the chaetotaxy of the head of the last stage larva is precisely the same as that of the first instar larva. In many of the specialised *Ditryisia*, e.g., SPHINGIDAE, LYMANTRIIDAE, numerous additional setae which have a general distribution are present after the first or succeeding moults; and it is these setae which are known as secondary setae. Similarly, secondary punctures would be those confined to the more specialised families of the order and even in those not present in the first instar. A further category, subprimary setae, is known to occur on the thorax and abdomen of even the most primitive families. Subprimary setae are few in number, definite in position, and are always present in the second instar but never in the first. Subprimary setae or punctures have not yet been recognised on the head of any caterpillar.

Owing to the fact that the primary setae and punctures of the head are fairly constant in number and position, though nevertheless sufficiently variable in both these respects to provide important diagnostic features for the separation of species and even families, various attempts have been made to give them all names. As a result of the efforts of a number of workers, the nomenclature of the cranial setae is now on a fairly stable footing and although agreement on the names to be used is general it is not universal, so that it seems desirable to give a brief review of the various attempts that have been made to evolve an adequate nomenclature. This is also made necessary as a few minor changes are proposed here.

So far as I am aware, Dyar (1896) was the first to name and use in any detail the cranial setae as an aid in distinguishing larvae. Dyar recognised 11 primary setae visible from a dorsal view, and he gave Roman numerals to these, numbering them from the hind margin forwards. Dyar's system of nomenclature was followed by Forbes (1910), Fracker (1915), and others. The next important advance in achieving an adequate nomenclature for the setae was due to Dampf (1910), who first showed that the setae form natural groups within certain cranial areas, and he named the groups of setae after the areas on which they were located. Dampf did not name the individual setae or punctures. A few years later in an important paper Heinrich (1916) gave names to all the setae and punctures except those of the vertical group. In addition, Heinrich re-defined Dampf's dorso-lateral group so that one of the setae (P1)

included by Dampf in the latter group was included by Heinrich in the posterior or postero-dorsal group and another (L1) was removed to the lateral group. In two subsequent papers Heinrich (1918, 1921) simplified the abbreviations of the names of the setae, e.g., Ad.-1 became A-1, and reversed his previous order of naming the ocellar setae.

In his study of Agrotid larvae, Ripley (1923 : 15) proposed a system of nomenclature which is in essence but an extension of that used by Dyar and Forbes. Ripley was unable to accept the nomenclature proposed by Dampf and Heinrich for fear that, "... in various families in which the trend of specialisation has been divergent this grouping relation may be altogether different." That this fear expressed by Ripley is without foundation is clear from a consideration of the divergent types of head illustrated in figures 2-9, which show that the groups of setae maintain their essential spatial relations to each other. The setal groups of such different forms as the prognathous leaf-mining larva of *Eriocrania* can be readily homologised with those of the hypognathous free-living larva of *Pieris*. Fortunately, Ripley's modification of Dyar's nomenclature has not been accepted. In his keys to Agrotid larvae, Crumb (1934) used the system of Heinrich.

Finally, the last important paper published on the setal nomenclature of the head is that of Gerasimov (1935). Gerasimov accepted the names proposed by Heinrich (1916), together with the slight changes introduced by Heinrich in 1918 and 1921. The only striking addition made by Gerasimov was to give names to the three setae and puncture of the vertical group.

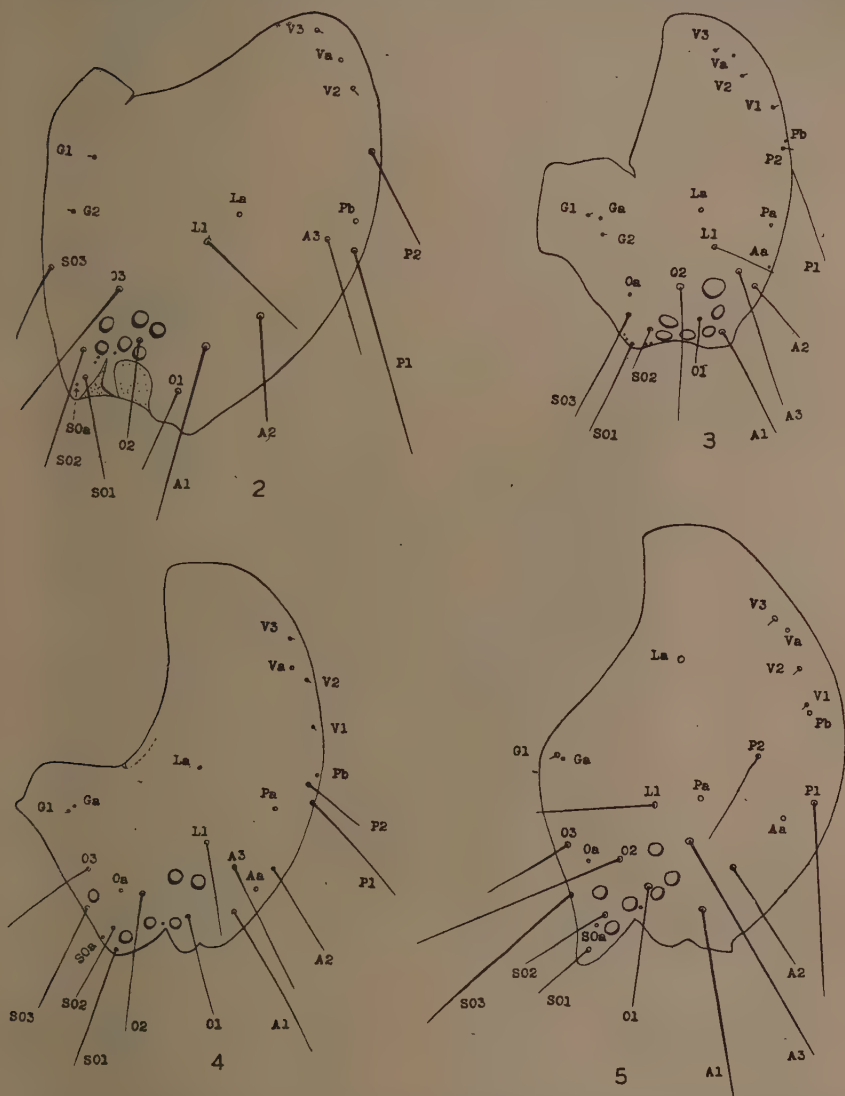
The names of the setae and punctures adopted here are in nearly every instance those used by Gerasimov (1935). Gerasimov chose the larva of the goat moth, *Cossus cossus* L., to illustrate his system of cranial setal nomenclature. *Cossus* (fig. 5) is exceptional in several particulars, and for this reason was an unfortunate choice. *Cossus* is unusual in having puncture Aa placed very far back so that it is nearer to P1 than to A2; and Gerasimov was therefore persuaded to include it in the posterior group as Pb with the result that he has called Pb puncture Va and Va puncture Vb. A further result is that, according to Gerasimov, *Cossus* lacks the very persistent Aa puncture. Heinrich (1916) has already drawn attention to the fact that puncture Aa (Ad-2a of Heinrich) revolves almost completely around seta A2, and this is substantiated by my own studies.

Even if Gerasimov were correct in calling Aa puncture Pb, his Va (my Pb) is most unfortunately named. A study of many different families shows that this puncture is almost invariably more closely associated with the posterior than with the vertical group of setae, and in the most primitive known Lepidoptera, ERIOCRANIIDAE, as well as in most of the highly specialised Ditrysiæ, e.g. PIERIDAE (fig. 9), AGROTIDAE (fig. 8), etc., it lies between and more or less in a line with P1 and P2. In many Microlepidoptera Pb (Va of Gerasimov) is slightly caudad from P1 and P2, but, so far as I am aware, only in *Cossus* is it nearer to V1 than to P2.

In all three monotreme, aculeate families examined, viz. : ERIOCRANIIDAE, ADELIDAE, and HEPIALIDAE, there were two minute genal setae which I have named G1 and G2 respectively. In all Ditrysiæ there was but a single genal seta which both Gerasimov and I call G1 although it is not clear if this seta is homologous to G1 or to G2 of the Monotrysiæ and Daenonypha.

In addition to the 12 long and four (rarely five) minute setae and eight punctures which occur very generally throughout the Lepidoptera, a few primary accessory punctures are found in some. One of these, which occurs frequently,

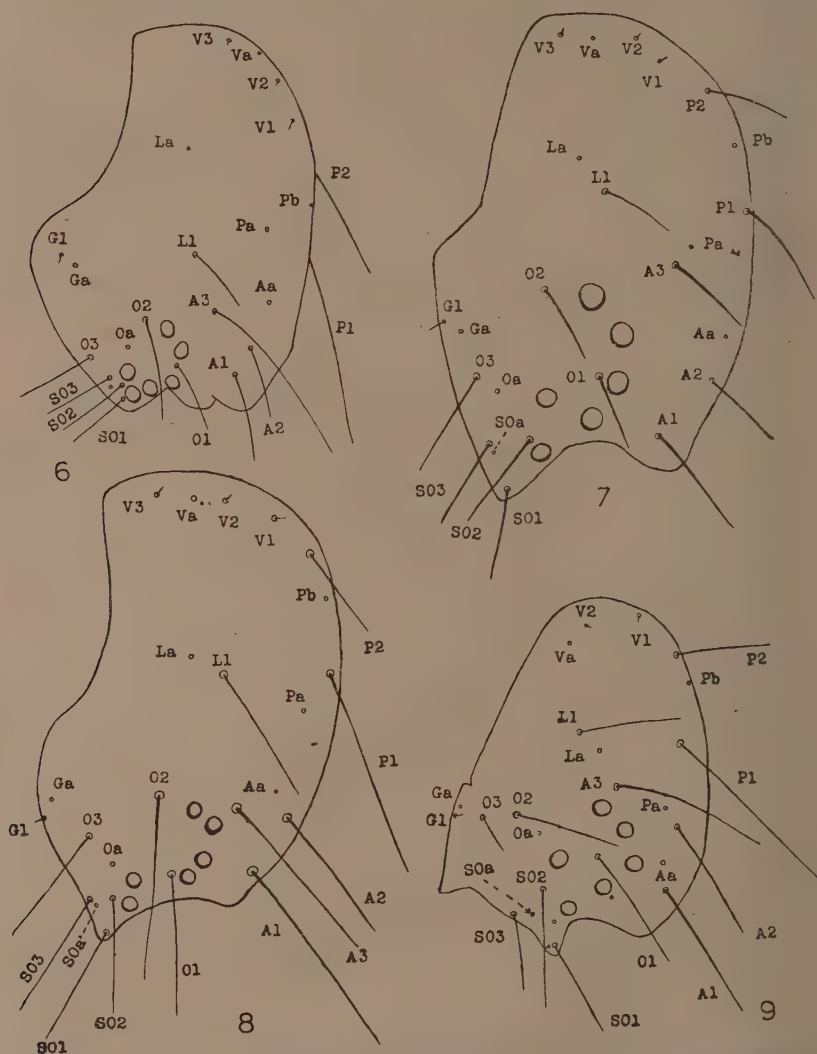
is associated with the fourth ocellus, and is present in such widely separated forms as *Hepialus* (fig. 2), *Cossus* (fig. 5), and *Pieris* (fig. 9). Others frequently occur



FIGS. 2-5.—The chaetotaxy of the head of lepidopterous larvae. (2) *Hepialus humuli* L. (3) *Adelidae*. (4) *Nemapogon ruricolella* Stainton, *TINAEIDAE*. (5) *Cossus cossus* L.

near or beneath seta S03. Gerasimov has named these Ob, SOb, and SOc, but at present there seems to be little point in adding further names to an

already cumbersome nomenclature, particularly as these punctures appear to be of little taxonomic importance and their positions can in any event easily be defined with great accuracy in relation to the ocelli and already named setae



FIGS. 6-9.—The chaetotaxy of the head of lepidopterous larvae. (6) *Dicymolomia julianalis* Walker, CRAMBIDAE. After Heinrich. (7) GEOMETRIDAE. (8) AGROTIDAE. (9) *Pieris brassicae* L., first instar.

and punctures. In two other slight particulars the nomenclature I have adopted differs from that of Gerasimov. I have called his Fr. 1. 1 and Fr. 1. 2 (Adf. 1 and Adf. 2 of Heinrich) AF1 and AF2 respectively, and for his C1 1

and his C1 2 I use C1 and C2 respectively. In Table 1 is shown the relation between the more important systems of nomenclature that have been proposed for the cranial setae.

The general uniformity of pattern exhibited by the cranial setae is remarkable and is unknown in any other order of insects which approaches the Lepidoptera in number of species. While it is true that there are a number of higher families in which the head of the later instars is densely clothed with conspicuous secondary setae and also some specialised leaf-mining forms as *Opotege* in which,

TABLE 1.

The names of the cranial setae according to different authors.

Dyar, 1896 Forbes, 1910	Heinrich, 1916	Ripley, 1923	Gerasimov, 1935	Hinton
IX	Anterodorsal Ad-1	Seta of vertex V9	Anteriores prima A1	A1
VIII	" Ad-2	" V8	" secunda A2	A2
IV	" Ad-3	" V4	" tertia A3	A3
—	" Ad-2a	Sensorium of vertex SV3	Porus anteriores Aa	Aa
VII	Ocellar O-3	Seta of vertex V7	Ommatalis prima O1	O1
V	" O-2	" V5	" secunda O2	O2
—	" O-1	" V6	" tertia O3	O3
—	" O-1a	—	Porus ommatalis Oa	Oa
—	—	—	" " Ob	(not named)
XI	Subocellar SO-1	Seta of vertex V11	Subommatalis prima SO1	SO1
VI	" SO-2	" V12	" secunda SO2	SO2
X	" SO-3	" V10	" tertia SO3	SO3
—	" SO-2a	—	Porus subommatalis SOa	SOa
—	—	—	" " SOb	(not named)
—	—	—	" " SOc	(not named)
III	Lateral L-1	Seta of vertex V3	Lateralis L1	L1
—	" L-1a	—	Porus lateralis La	La
II	Posterodorsal Pd-1	Seta of vertex V2	Posteriores prima P1	P1
I	" Pd-2	" V1	" secunda P2	P2
—	" Pd-1a	Sensorium of vertex SV2	Porus posteriores Pa	Pa
—	" Pd-2a	" " SV1	" " Pb	Pb
—	Secondary tubercles	Occipital seta O3	Verticalis prima V1	V1
—		" O2	" secunda V2	V2
—		" O1	" tertia V3	V3
—		Occipital sensorium SO	Porus verticalis Va	(= Pb) Va
—	Genal G-1	Seta of vertex V13	Genalis G1	G1
—	Genal G-1a	Postgenal sensorium PAS	Porus genalis Ga	G2 Ga
—	Fr.-1	Frontal seta F1	Frontalis F1	F1
—	Fr.a	" sensorium FS	Porus frontalis Fa	Fa
—	Adf.1	Adfrontal seta A2	Fronto-lat. prima Fr.1.1	AF1
—	Adf.2	" " A1	" secunda Fr.1.2	AF2
—	Adf.a	" sensorium ADS	Porus fronto-lat. Fr.1.a	AFa
—	Ep. 1	Clypeal seta C2	Clypealis prima Cl1	C1
—	Ep. 2	" C1	" secunda Cl2	C2

in some species, the mature larva may have the cranial setae reduced to three, it is nevertheless noteworthy that the fundamental setal pattern is the same in all first instar larvae known and also the same in the later instars of the vast majority of the species. Figs. 2-9 show that the long setae, which undoubtedly function as tactile organs, are rather evenly distributed over the anterior parts of the head. The proportional extent of the anterior areas on which the long setae occur is, however, subject to considerable variation (cf. figs. 5 and 9). The long setae are more or less confined to those parts of the head which are not normally retracted into the prothorax. A nearly prognathous head, such as that of *Cossus* (fig. 5), which can be deeply retracted into the pro-

thorax has a relatively small area (about $\frac{1}{2}$) clothed with long setae and a relatively large area from which long setae are absent. A highly developed hypognathous head, such as *Pieris* (fig. 9), which can hardly be retracted into the prothorax, has a relatively very large area clothed with long setae and only a relatively small area from which these setae are absent. The general preservation of the primitive pattern throughout the Lepidoptera is probably due to the fact that already in the most primitive forms there was a fairly even distribution of tactile setae on the exposed parts of the head, and changes in response to different environmental needs in different groups were chiefly reflected in slight changes of position and relative lengths of the setae rather than in the acquisition of new setae or the total disappearance of those already present. The notable exceptions to this generalisation have already been mentioned above.

The parts of the vertex and the sides of the head which are retracted into the prothorax nearly always have only four or five very minute setae on each side : three on the vertex and one or two on the caudal part of the gena. It appears probable that these minute setae function as proprioceptors ; and further evidence for this view is given below when dealing with the minute setae of the thorax and abdomen. In forms such as *Eriocrania*, where the head is greatly lengthened and almost entirely retracted into the prothorax, setae F1, AF1, AF2, P1, P2, A2, A3, L1, O2, and O3 are as short as those of the vertical and genal groups and may also serve the same purpose. It is probably also not without significance that V3 is lost in such hypognathous forms as *Pieris*, where the head is scarcely retracted into the prothorax.

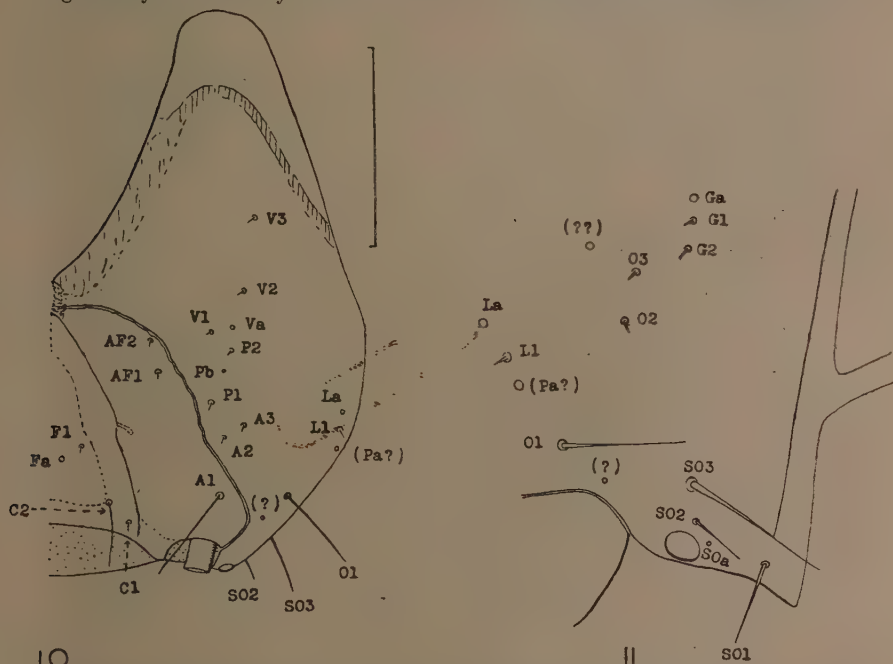
An examination of a large number of heads of unrelated caterpillars shows that not only are the number and position of groups of setae very constant, but also that the relative lengths of the setae themselves are very constant. A brief description of the relative lengths and positions of the setae within their groups will be useful in identifying the setae in species where they are abnormally distributed.

The clypeal setae, C1 and C2, are more or less equal in length, and C2 is always caudad from C1 and nearer the medial line. *Eriocrania* has C1 very much shorter than C2 (fig. 10), but in this discussion extreme modifications, such as occur in some of the leaf-miners, are omitted. The frontal puncture is always mesad from F1 and at about the same level or slightly below, except in the *HEPIALIDAE*, where it is very close but laterad from F1. The frontal seta is usually as long as the clypeal setae. The adfrontal setae are nearly always shorter than F1 or C1 and C2, and AF2 is frequently slightly shorter than AF1. AF2 is always behind and slightly mesad from AF1, and their position on the adfrontals, as well as their distance from each other, varies considerably and provides useful characters for distinguishing genera and higher taxonomic categories. AFa is usually about half-way between AF1 and AF2 but is sometimes absent (*HEPIALIDAE*, some *ERIOCRANIDAE*) and sometimes below AF1 (some *TINAEIDAE*).

The anterior setal group is most characteristic : A1 is nearly always distinctly longer than A2, which is behind and usually laterad from the former, and A3 is nearly always at least as long as A1 and behind and laterad from A2, being usually close to the first ocellus. The position of Aa, as already stated, is very variable, and this puncture may be found behind A2, above it, or between A2 and A1. In the *ERIOCRANIDAE* the position of A1 is unique in the sense that it occurs (of course only in older larvae) on the adfrontal sclerite. The adfrontal sclerite of the *Dacnonypha* is enormously broad and includes the region directly

behind the antenna (fig. 10), so that in relation to the antenna A1 is not abnormally placed.² The position of the anterior group in the *HEPIALIDAE* (figs. 2, 13) appears to be unique, the three setae being in a line roughly parallel to the long axis of the head so that A3, which is scarcely longer than A2, is more caudad than P1.

Of the three setae comprising the ocellar group, O1 is usually as short as A2 or shorter, O2 is long, often as long as A3, and O3 is as short or shorter than O1. Seta O1 is nearly always very close to the third and fourth ocellus, O2 is generally considerably behind and more or less at the level of the fifth ocellus



FIGS. 10-11.—The chaetotaxy of the head of *Eriocrania* sp. (*E. sangi* Wood?). In the *Eriocraniid*, *Chapmania sparmannella* Bosc. AF1, AF2, and AFa are all present according to Grandi (1933).

whereas O3 is below the ocelli and slightly anterior to O2. Puncture Oa is very variable in position. It usually lies between O1 and O2 slightly anterior to a line drawn between these setae, but in a few, e.g. *Pieris* (fig. 9), it may actually be above O2 and between the latter and O1. In the *HEPIALIDAE* Oa is absent, at least in those examined. In addition to Oa, a further puncture is often present near or between the third and fourth ocelli.

² In this connection it should be noted that Fracker (1915: 60) has based his description of the family characters of the *MICROPTERYGIDAE* on a larva thought by him to be that of *Epimartyria auricrinella* Walsingham. This larva is, however, obviously that of a species of *Mnemonica* Meyrick, a genus very near to *Eriocrania*. In his key to the families, the name *ERIOCRANIIDAE* should replace the name *MICROPTERYGIDAE*. It should also be noted that in his key the *ERIOCRANIIDAE* (his *MICROPTERYGIDAE*) are distinguished from the *GRACILLARIDAE* and *NEPTICULIDAE* on the position of the ocellus, which is approximately the same in all three families.

The position of the subocellar setae (figs. 2-9) is more constant than any except the clypeal, frontal, and adfrontal groups. In *Eriocrania* SO3 is unusual in being higher than SO2. In *Hepialus* it is exceptionally far back. Puncture SOa is near and below SO2. Additional punctures are not uncommon in the area of the subocellar setae. A puncture is often present near the fifth ocellus. In the HEPIALIDAE and ADELIDAE there are two punctures in this position. One or two punctures are also often present near or actually below SO1. The lateral seta may be near or considerably behind the ocelli, but it is generally at the level of the first ocellus. As a rule, it is distinctly shorter than A3, to which it is often near. Puncture La is more or less directly behind L1 but exceptionally may be antero-dorsal to it (fig. 9). It may be near L1 as in some AGROTIDAE (fig. 8) or very far behind as in *Cossus* (fig. 5). Of the posterior group, P1 is commonly the longest seta of the cranium, and it is near the adfrontal suture. P2 is a very much shorter seta which varies from being directly ventrad from, to directly behind, P1. Puncture Pa is generally more or less between L1 and P1. It is often close to L1, but rightly appears to belong to the posterior group. In *Gnorrimoschema* and *Nealydia*, as shown by Heinrich (1916: 160), it is between P1 and P2 and very close to Pb. Puncture Pb is behind and slightly to considerably ventrad from P1. Usually it is between P1 and P2, but when P2 is laterad from P1, Pb is caudad from P2 although it is very rarely (*Cossus*) nearer to V1 than to P2.

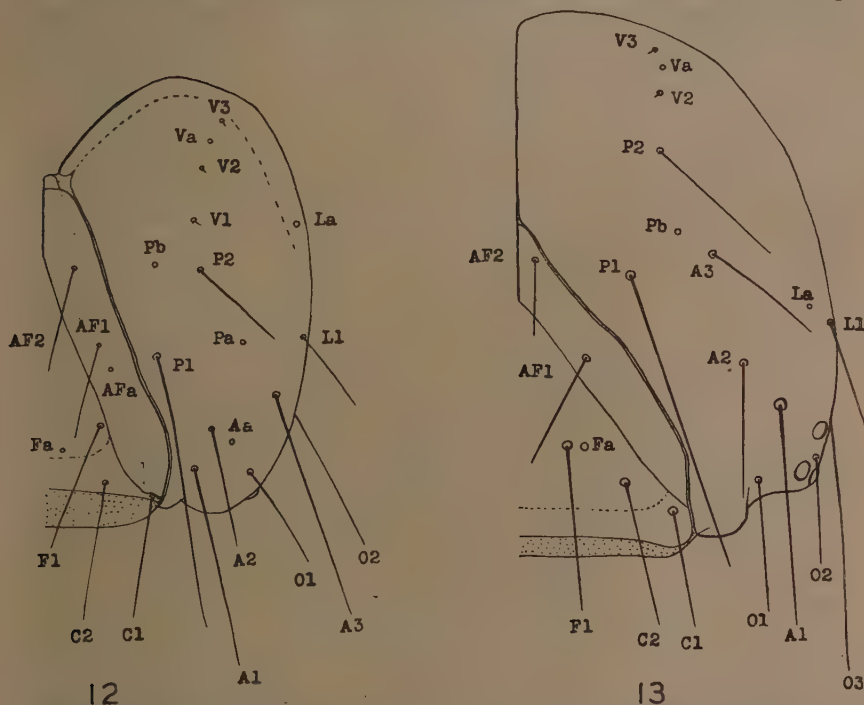
The minute setae of the cranium, those which probably function as proprioceptors, occur in two widely separated groups: a vertical group and a genal group. The three vertical setae are always in a line or wide angle curve which posteriorly diverges from the medial line in prognathous forms. As the head becomes increasingly hypognathous, a line joining the vertical setae shifts laterally so that in such well-developed hypognathous forms as *Pieris* the vertical setae form a row which is at right angles to the medial longitudinal line of the head. One of the vertical setae is very occasionally absent. In *Hepialus* it is probably V1 and in *Pieris* V3. Puncture Va is usually between V2 and V3, but in *Eriocrania* it is between V1 and V2. The genal group consists of one or two setae and a puncture. In all Daconypha and Monotrysia of which I have had material two genal setae are present, but Heinrich (1918) has illustrated only one genal seta in the TISCHERIDAE and NEPTICULIDAE, which are leaf-mining monotremes. In all Ditrysia known to me only a single genal seta is present. Puncture Ga is absent, so far as I know, only in the HEPIALIDAE. This puncture is generally very near to G1, but it is otherwise very variable in position, revolving completely around G1.

In the general account given above of the normal disposition of the cranial setae, it has been noted that *Hepialus* (and I presume all HEPIALIDAE, as the cranial setae of *Leto*, *Charagia*, and *Oncopera* are nearly identical to those of *Hepialus*) departs widely from the usual type found in the Lepidoptera. For instance, in the arrangement of the cranial setae *Hepialus* differs more from other Monotrysia such as Nepticulids and Adelids than do the latter families from such specialised Ditrysia as the PIERIDAE (first instar), GEOMETRIDAE, AGROTIDAE, etc. This is not to imply, of course, that the PIERIDAE, for example, are nearer the Adelids than are the Hepialids. Such a view cannot be held for an instant when the characters of all stages are taken into account.

The view that the HEPIALIDAE are, with the exception of the ERIOCRANIIDAE, the most primitive family of the Lepidoptera is widely held by entomologists, some of whom appear to have few qualms in deriving the remainder of the Lepidoptera directly from them. Amongst the Lepidoptera in which the bursa

copulatrix does not have a separate external opening and in which aculei are present between the wing scales, the *HEPIALIDAE* have departed, in their own direction, as far from the archetype of the *Lepidoptera* as the *TISCHERIDAE* and *NEPTICULIDAE*. In the phylogenetic charts or trees of Busck (1914, 1932) the *HEPIALIDAE* are placed in far too primitive a position. In the latter paper Busck (1932) actually places them below the *ERIOCRANIIDAE*.

Only as regards some of the larval characters, e.g. loss of thoracic legs, which are, however, clearly the result of specialisation attributable to their leaf-mining



FIGS. 12-13.—The chaetotaxy of the head. (12) *Tinaea pallescentella* Stainton. (13) *Hepialus humuli* L.

habits, can the *ERIOCRANIIDAE* be considered to be less primitive than the *HEPIALIDAE*. In respect to all other characters which differ in the two families, it is clearly the *HEPIALIDAE* which are the more specialised. The *HEPIALIDAE* have one of the most advanced incomplete pupae yet known amongst the *Lepidoptera*. The seventh abdominal segment of the male is solidly fixed to the eighth,³ an evolutionary advance rarely achieved amongst other forms

³ The seventh segment of the male pupa of *Leto* is certainly not movable. In some *Hepialus* spp. it appears to be very slightly movable, but has nothing like the degree of mobility of the sixth, as the "intersegmental" membrane between the seventh and eighth segments is very nearly as hard as the general cuticle of these segments. That the pupa is highly specialised is emphasised by Mosher (1916 : 38) although she believes the seventh of the male is movable. It should be noted that the pupa lacks maxillary palpi though even in such *Ditrysia* as the *SESIIDAE*, which have only minute maxillary palpi in the adults, the maxillary palpi of the pupa are very large. As the maxillary palpi appear to persist for

possessing an incomplete pupa but nearly universal in those higher Ditrysia (*Chrysocorys* and *Epermenia* are the only exceptions known as yet) which have a truly obtect pupa. The ERIOCRANIIDAE have a free pupa with functional mandibles which is similar to that of the Neuroptera-Planipennia, Mecoptera, Zeugloptera, and Trichoptera. In contrast to the Eriocraniids, adult Hepialids have no lateral ocelli,⁴ or vestigial maxillary palpi, and in some genera the labial palpi are only 2-segmented. A further specialisation of the Hepialids should be mentioned in this connection. According to Chapman (1913) the female *Hepialus* has lost all trace of the eighth abdominal spiracle, whereas in both the male and female of *Eriocrania* the eighth abdominal spiracle is open.

It seems certain that the recent HEPIALIDAE⁵ arose from a group which had advanced considerably from the ancestral Eriocraniids in respect of pupal and adult structure but still retained the jugum or fibula. I would put the point of origin of the Hepialoidea before the separation of the ancestors of the Monotrysia with a hard piercing ovipositor (PRODOXIDAE, HELIOZELIDAE, INCURVARIIDAE, ADELIDAE) from the ancestors of those which retained the soft non-piercing type of ovipositor (TISCHERIDAE, NEPTICULIDAE, OPOSTEGIDAE). This point would be some distance above the point at which the ancestors of the ERIOCRANIIDAE separated off from the archetype of the Lepidoptera. No other families can be derived from the Hepialoidea or even from their fairly remote ancestors in view of the fact that the Hepialoidea represent an end line highly specialised in certain directions peculiar to themselves.

THORACIC AND ABDOMINAL SETAE.

Although a number of different systems of naming the setae of the thorax and abdomen have been proposed, usually only the authors have been in their favour, and only two systems are now in use: an extension of Dyar's (1894) system of Roman numerals and Fracker's (1915) system of Greek letters. Of these two systems, Dyar's is the more widely used, but very few workers use either, or, indeed, any system at all. Those interested in the various attempts that have been made to name the setae are referred to Gerasimov's (1935) paper, where the different systems are compared in tabular form. Most of the previously proposed nomenclatures have failed to gain general acceptance because of the length and clumsiness of the names used, the omission of a number of primary setae, and the obviously incorrect homologies suggested. The systems of Dyar and Fracker, unsatisfactory though they are in many respects, have nevertheless the great advantage of employing short symbols for the setae and being already in use. It is, therefore, with considerable reluctance that I here propose still another system. However, it may be truly said that so little has yet been done in the way of describing lepidopterous larvae that the confusion

some time in a lepidopterous pupa after they have become vestigial in the adult, it probably follows that where maxillary palpi are lacking in the pupa or greatly reduced their absence or great reduction in this stage may be regarded as evidence that their loss or reduction in the adult is of some antiquity.

⁴ The ocelli are sometimes (*e.g.* Forbes, 1923) stated to be rudimentary. Such genera as *Zelotypia* have tubercles in the position in which ocelli would be expected to be found. These tubercles are probably Jordan's Organ, in which the ocellar nerve persists but the pigment and lens have been lost. Jordan's Organ is not a photoreceptor.

⁵ The Australian ANOMOSEIIDAE and PALAEOSTIIDAE as well as the South African PROTHEORIDAE belong to the superfamily Hepialoidea. Nothing is known of the larvae or pupae of these families, but, judging from the published accounts of adult structure, they are all specialised offshoots of a stock which gave rise to the more generalised HEPIALIDAE.

a new system is bound to cause will soon be offset by the gain in the ease and accuracy of descriptive work that a better system will occasion.

The objections to Dyar's system may be briefly stated. The use of Roman numerals precludes the use of numerals for the segments of the body. Usually Roman numerals are used to designate the three thoracic segments and Arabic numerals to designate the abdominal segments. By using numerals for the body segments descriptions of species can be greatly condensed. It has already been pointed out by Fracker that a series of names which have as definite an order as numbers is misleading and likely to lead to prejudiced opinions on homology, particularly as a number of setae revolve almost completely around each other. For example, one genus may have the setae in the usual order, I, II, III, IV, beginning at the medio-dorsal line, and another may have the homologous setae arranged II, I, IV, III, and so on. The use of numbers for the setae, like the use of numbers for the wing veins, has often been a chief cause of faulty homologies. Instances of this are given in a later section. And, finally, it should be pointed out that, in any case, if Dyar's system was adopted here—even including the additions and corrections of Gerasimov and others—very many changes would be necessary in view of my different concept of the homologies of many of the setae.

There are some most serious objections to the use of Fracker's system. Fracker failed to discover in most of the species he described the existence of three primary setae on the prothorax, six on the mesothorax, six on the metathorax, and two on each of the first nine abdominal segments. Thus a total of 33 primary setae are overlooked in the vast majority of the species he described. A further objection to his system is that some of the homologies he suggests are incorrect, and the pains he has taken to make his classification of the larvae fit the division of the order into Jugatae and Frenatae—a very unnatural division—have led him to discover differences which do not exist between *Hepialus* and the remainder of the Lepidoptera. Fracker's choice of letters as names for the setae makes it possible to avoid disarranging the whole of his system when new concepts of the homologies of some of the setae are introduced. Nevertheless, the many additions to the number of primary setae made here, as well as the numerous changes in homology that now appear necessary, would so alter his system that the opportunity is taken of discarding it altogether. A purely practical, but for all that considerable, disadvantage of a system of Greek letters is that few entomologists have access to a typewriter with the necessary keys.

The present study has shown that there are two very different kinds of setae on the body of a caterpillar. The two kinds differ nearly always in size and length, position, and, almost certainly, function. Furthermore, the number and position of the two kinds of setae vary independently of each other. That there are two kinds or categories of setae on the thorax and abdomen has not been clearly recognised before, and, as one consequence of failure to discriminate between them, setae of one category have often been homologised with those of the other.

(A) *The microscopic or proprioceptor setae.*

Near the anterior margin of most segments of the thorax and abdomen and near the posterior margin of the dorsum of the prothorax are a few very small, microscopic setae which come in contact with the segment in front or may be entirely concealed by it when there is any telescoping or retraction of one segment into another such as usually accompanies most normal movements of the

larva. Owing to their position and size, it seems very likely that these setae, like those of the vertical and genal groups of the head, function as proprioceptors rather than as tactile receptors for external stimuli. Whether or not this is later proved or disproved in no way affects the homologies suggested here. For the sake of convenience, these setae are henceforth referred to as microscopic or proprioceptor setae in contradistinction to the long or tactile setae; and symbols for their groups are always preceded by a capital "M", e.g. MD1, MSV1, etc. Very occasionally one or more of the microscopic setae is greatly lengthened, so that in all outward parts it is indistinguishable except in position from one of the long or tactile setae. This change in length is no doubt accompanied by a change in function. Such changes in length, however, occur rarely and are so easily recognised as such that in the interest of convenience and clarity the two systems of setae are dealt with separately.

The microscopic setae are all primary; and they are nearly identical in number and position throughout the order. Furthermore, with successive moults there is no change in their number or significant change in their position, so that in respect to these setae the last instar larva is precisely the same as the first instar larva. In many of the more recent Ditrysia, which have a dense coating of secondary hair, it is difficult or even impossible to distinguish between the microscopic setae and the finer secondary setae, but they are clearly recognisable in such hairy forms as the mature larvae of some Arctiids.

The distribution of the microscopic setae is shown in Tables 3-4, which include species from a sufficiently large number of the most primitive as well as the most specialised families to make generalisations tolerably safe. The distribution of the microscopic setae is the same in the leaf-miner *Eriocrania* (presumably also in its first instar) as in the specialised arboreal *Sphinx*, two forms whose common ancestor was not later than the beginning of the Cretaceous or, in other words, two forms which have had no connection with each other for at least 110 million years. The position of the microscopic setae on the thorax and abdomen and their relation to the tactile setae is shown in figs. 14-22.

(1) The thoracic microscopic setae or proprioceptors.

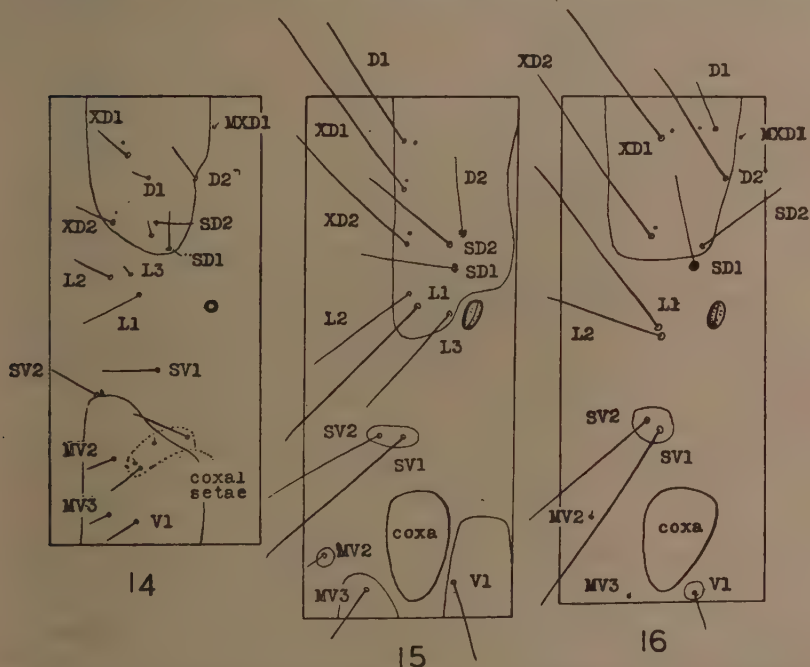
On the side of the caudo-dorsal margin of the prothorax there is a minute seta, MXD1, which may be actually on the sclerotised thoracic shield or on the membranous region behind it. This seta has been homologised with MD1 of the metathorax by Tsou (1914), who had in mind the bisetose MD group of the metathorax of the AGROTIDAE and accounted for the unisetose MD group of the mesothorax of the same family by suggesting that MD of the mesothorax was originally bisetose but one of the setae had migrated on to the prothorax. Forbes (1916), Ripley (1923), and Gerasimov (1935) have accepted Tsou's explanation. Apart from the fact that no other evidence has yet been produced of any seta migrating from one segment to another, the bisetose group of the metathorax occurs only amongst the most advanced Ditrysia and in these only in the AGROTIDAE, ARCTIIDAE, and related families. In *Eriocrania* and the Monotrysia, as well as all the Microlepidoptera⁶ which have been studied, MD of the metathorax is invariably unisetose like MD of the mesothorax. There is, therefore, every reason for believing that the second seta of the metathoracic MD group has been evolved as a new or additional seta in the Agrotoidea. The bisetose MD group of the metathorax provides an interesting confirmation of

⁶ Throughout this paper the convenient term Microlepidoptera is used to include the Ditrysia below the Rhopalocera and Macroheterocera or moths whose larvae have, at least in the final instar, the crochets of the prolegs arranged in a mesoseries.

the relationship of the AGROTIDAE, LYMANTRIIDAE, LITHOSIDAE, ARCTIIDAE, THAUMETOPOEIDAE, NOTODONTIDAE, etc., previously established on the structure of the adults and the common possession of an upright type of egg.

In the HEPIALIDAE, in *Pieris*, and undoubtedly others, MXD1 is absent. This is to be regarded as a specialised and not a primitive condition. The absence of MXD1 in the HEPIALIDAE is further evidence of the degree of specialisation achieved by this primitive family.

Two prothoracic setae, XD1 and XD2, have been homologised by Gerasimov (1935) with some of the microscopic setae of following segments and by others with some of the long tactile setae. The opinions which have

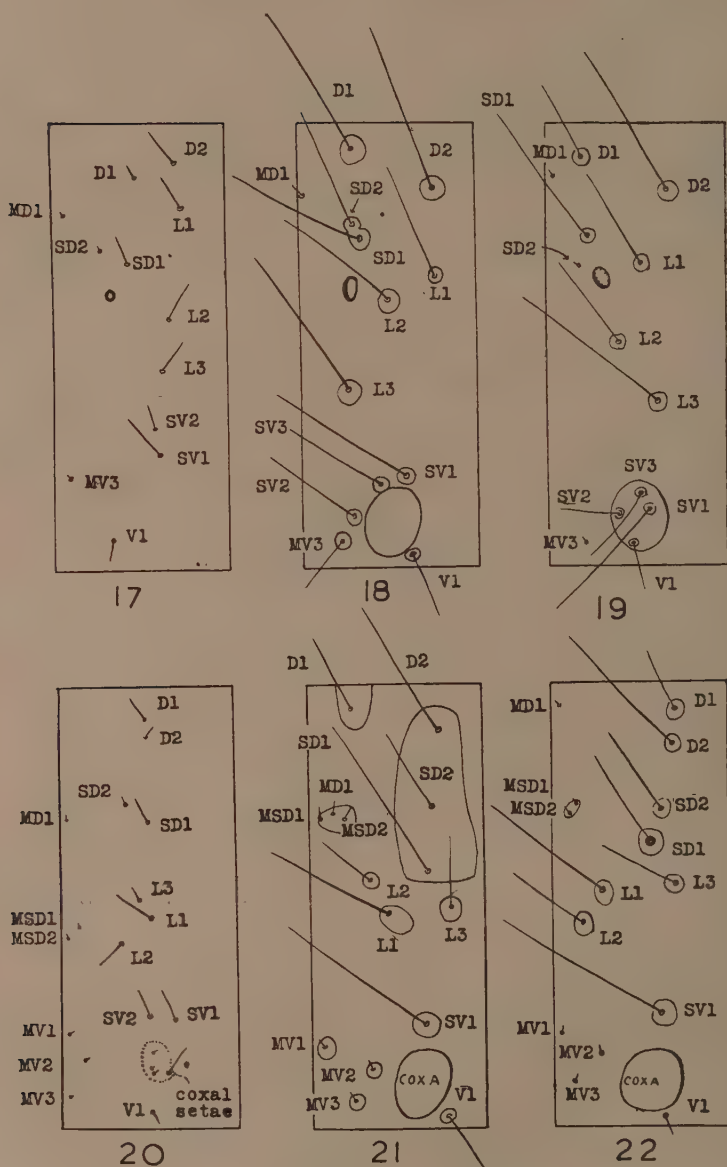


FIGS. 14-16.—The chaetotaxy of the prothorax. (14) *Eriocrania* sp. (*E. sangi* Wood?). (15) *Hepialus humuli* L. (16) *Hadena didyma* Esper, AGROTIDAE.

been held regarding these two setae are shown in fig. 23. For reasons that are discussed when dealing with the tactile setae, it appears certain that XD1 and XD2 are not the homotypes of any of the long setae of other segments, and on this point I am in complete agreement with Gerasimov (1935).

It thus appears that only two views are possible as regards the homology of the XD group: (1) they are the homotypes of the proprioceptors of the meso- and metathorax, or (2) they are new or additional tactile setae developed in response to special needs not affecting the anterior margin of the two caudal thoracic segments.

The first of these views is, as has already been stated, that of Gerasimov, which he would hardly have put forward had he considered the functions of the two kinds of setae. Above the base of the coxa of the meso- and metathorax



FIGS. 17-22.—The chaetotaxy of the sixth abdominal segment and the mesothorax. (17) Sixth abdominal segment of *Eriocrania* sp. (18) Same of *Hepialus humuli* L. (19) Same of *Hadena didyma* Esper, AGROTIDAE. (20) Mesothorax of *Eriocrania* sp. (21) Same of *H. humuli* L. (22) Same of *H. didyma* Esper.

there are never less than three microscopic setae. If the two XD setae are homotypes of these, it still remains necessary to account for one missing microscopic seta, and, furthermore, there is obviously no means of saying which of the three are to be regarded as the homotypes of the XD setae. But more telling still, is the fact that the microscopic setae are only developed on the parts of the body segments which can be and are telescoped or retracted into others or which are covered by parts of the legs. The only exception to this is the absence of proprioceptors on the tenth tergite. Now the anterior margin of the pronotum differs strikingly from the anterior dorsal margin of the two posterior thoracic segments by virtue of the fact that the two latter are frequently retracted into the preceding segments, whereas the anterior margin of the pronotum cannot be retracted in a similar manner into the head. On the contrary, it is always the posterior part of the head which is retracted into the

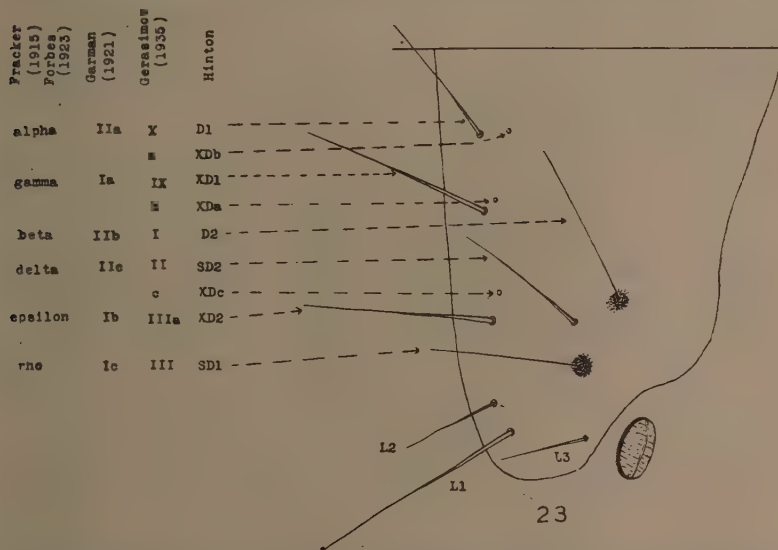


FIG. 23.—The nomenclature of the setae of the prothorax of the HEPALIDAE according to different authors. The nomenclature of Garman is adjusted from the COSSIDAE.

prothorax. And it is precisely on this posterior part of the head that proprioceptors are developed.

My own opinion is that the two XD setae are neither the homotypes of the microscopic setae of other segments nor still less are they the homotypes of any of the tactile setae, but are a special group developed only on the anterior margin of the prothoracic plate. It has already been pointed out that when a primitive or prognathous head, such as that of the goat moth, is exerted, the basal half of the head is armed solely with minute proprioceptors. If there were no XD setae on the anterior margin of the pronotum, a very considerable area, *i.e.* from the anterior half of the head to the prothoracic D and SD groups of setae, would be left, as it were, unprotected by long tactile setae. The presence of the XD setae thus affords more or less complete protection that otherwise would be lacking to the neck and base of the head. Put another way, it may be said that

the XD setae have been evolved through selection because the part of the head which is normally retracted in a primitive form cannot, for obvious mechanical reasons, develop long setae for its own protection.

On the prosternum are two microscopic setae which I have named MV2 and MV3 on the assumption that the most ventral of these is the homotype of MV3 of the two posterior thoracic segments and MV3 of the first nine abdominal segments. In all species examined MV1 is absent, which is most surprising in view of its absolute constancy on the meso- and metathorax. A possible explanation of the absence of MV1 on the prosternum is that it is redundant in view of the fact that the part of the cuticle (by analogy with the meso- and metathorax) on which it has failed to develop is precisely that part which is generally brought in contact with the posterior genal region of the head where one or two (G1 or G1 plus G2) proprioceptors are always present. Seta MV2 is always antero-dorsad from MV3.

The absence of MV1 on the prosternum has led Gerasimov to suggest an

TABLE 2.

The subventral group of tactile setae and the ventral group of microscopic setae of the thorax and abdomen.

	PSYCHIDAE		HEPIALIDAE	
	Gerasimov	Hinton	Gerasimov	Hinton
Prothorax	VIIa	SV1	VIIa	SV1
"	VIIb	SV2	VIIb	SV2
"	VIIc	MV2	VIIc	MV2
"	VIIId	MV3	VIIId	MV3
Meso- and metathorax	VIIa	SV1	VIIa	SV1
"	—	SV2	—	—
"	VIIb	MV1	VIIb	MV1
"	VIIc	MV2	VIIc	MV2
"	VIIId	MV3	VIIId	MV3
Abdomen	VIIa	SV1	VIIa	SV1
"	VIIb	SV2	VIIb	SV2
"	VIIc	SV3	VIIc	SV3
"	VIIId	MV3	VIIId	MV3

interesting but incorrect series of homologies. On the abdomen of *Hepialus*, MV1 is large and close to the trisetose SV group of tactile setae, so that by Gerasimov MV1 was considered to be part of the SV group (his VII group), which thus comprised four setae. On the meta- and mesothorax of *Hepialus* and most Lepidoptera there is only one SV seta. Gerasimov detected the three MV setae which had previously been fairly regularly missed, and, as 3MV plus 1SV equals four, he was led to suppose that all these four were homologous to the 1MV plus 3SV setae of the abdomen. The truth of his homologies appeared to be confirmed by the fact that on the prothorax SV is always bisetose as is MV, so that 2SV plus 2MV equals four. That Gerasimov's interpretation is incorrect is evident from the condition obtaining in the TINAEINAE, PSYCHIDAE, some GALLERINAE, at least some NOTODONTIDAE, etc., where SV of both the meso- and metathorax is bisetose. In Table 2 the differences in our interpretation of these setae are shown.

On each side of the mesothorax near the anterior margin there is always one dorsal microscopic seta, MD1, more or less at the level of D2 and two, MSD1

and MSD2, microscopic setae more or less opposite SD1. Although MD1 is usually more or less at the level of D2, in a few forms it is as near the dorsal line as D1, but MD1 may also migrate a short distance ventrally so that it is not infrequently found near or with the MSD group. In the latter case it may actually be on the same pinnaculum as the MSD group when these have a common pinnaculum. Instances of this are common in the family TINAEDAE, where all degrees of the approximation of the MD and MSD groups are to be found. For instance, *Scardia boleti* Fabricius has MD1 opposite D2, *Tinaea*

TABLE 3.

The distribution of the microscopic setae on the prothorax and abdomen.

	Prothorax				Abdomen				
					first			second to ninth	
first instar	MXD1	MV1	MV2	MV3	MD1	MD2	MV3	MD1	MV3
PSYCHIDAE (<i>Fumea</i>) . . .	+	—	+	+	+	—	+	+	+
COSSIDAE (<i>Cossus</i>) . . .	+	—	+	+	+	—	+	+	+
SESIIDAE (<i>Sphecia</i>) . . .	+	—	+	+	+	—	+	+	+
PIERIDAE (<i>Pieris</i>) . . .	—	—	+	+	+	—	+	+	+
AGROTIDAE (<i>Hadena</i>) . . .	+	—	+	+	+	—	+	+	+
ACRONYCTIDAE (<i>Apatele</i>) . . .	+	—	+	+	+	+	+	+	+
LYMANTRIIDAE (<i>Euproctis</i>) . . .	+	—	+	+	+	—	+	+	+
NOTODONTIDAE (<i>Cerura</i>) . . .	+	—	+	+	+	+	+	+	+
SPHINGIDAE (<i>Sphinx</i>) . . .	+	—	+	+	+	—	+	+	+
mature larva									
ERIOCRANIIDAE . . .	+	—	+	+	+	—	+	+	+
HEPIALIDAE . . .	—	—	+	+	+	—	+	+	+
INCURVARIIDAE . . .	+	—	+	+	+	—	+	+	+
ADELIDAE . . .	+	—	+	+	+	—	+	+	+
TINAEDAE . . .	+	—	+	+	+	—	+	+	+
PSYCHIDAE . . .	+	—	+	+	+	—	+	+	+
COSSIDAE . . .	+	—	+	+	+	—	+	+	+
SESIIDAE . . .	+	—	+	+	+	—	+	+	+
TORTRICIDAE . . .	+	—	+	+	+	—	+	+	+
PYRALIDAE . . .	+	—	+	+	+	—	+	+	+
GEOMETRIDAE . . .	+	—	+	+	+	—	+	+	+
THYATIRIDAE . . .	+	—	+	+	+	—	+	+	+
AGROTIDAE . . .	+	—	+	+	+	—	+	+	+
ACRONYCTIDAE . . .	+	—	+	+	+	?	+	+	+
ARCTIIDAE . . .	+	—	+	+	+	—	+	+	+
LITHOSIIDAE . . .	+	—	+	+	+	—	+	+	+
LYMANTRIIDAE . . .	+	—	+	+	+	—	+	+	+
THAUMETOPOEIDAE . . .	+	—	+	+	+	+	+	+	+
NOTODONTIDAE . . .	+	—	+	+	+	+	+	+	+
SPHINGIDAE . . .	+	—	+	+	+	—	+	+	+

thecophora Walsingham has the pinnaculum surrounding MD1 nearly touching that of the MSD group, and *Tinaea uterella* Walsingham has the two groups on the same pinnaculum though MD1 is still easily distinguishable by its much more dorsal position on the common pinnaculum. In some (all?) *HEPIALIDAE* the relation of these two groups is unusual in that MD1 is between and nearly in line with MSD1 and MSD2. This is true of *Hepialus*, *Phassus*, *Leto*, and *Charagia*. Gerasimov has suggested that in the *HEPIALIDAE* one of the three belongs to the MD group, and I have no doubt whatever that he is correct.

⁷ In *Cerura vinula* L. there is an additional MXD seta on each side of the hind margin of the prothorax. This may be, however, only a secondary seta.

Although Fracker generally overlooked the existence of these setae, he did name those of *Hepialus humuli* L., homologising all three (MD1 + MSD1 + MSD2) with a single seta (XD2 or gamma) of the prothorax.

On each side of the mesosternum there are invariably three microscopic setae, of which the most dorsal, MV1, is apparently always the most anterior, and the most ventral, MV3, is usually more anterior than MV2. The positions of the three MV setae vary somewhat and can occasionally be of systematic value. The most caudad of these setae, MV2, can hardly function as a locator of the segment in front; and it seems very likely that it may function as a proprioceptor of the basal part of the leg—perhaps the femur, as the coxa has its own proprioceptors. In this connection, it is interesting to note that in *Eriocrania* (figs. 14, 20), which has lost its thoracic legs, MV2 and MV3 of the meso- and metathorax are relatively closer to the anterior margin than in forms possessing legs; and MV2 and MV3 may have thus begun to function, as the legs diminished in size and importance, as locators of the segment in front. On the prosternum of *Eriocrania*, MV2 and MV3 are relatively longer—as long as some of the tactile setae—and remain as far caudad as in forms possessing legs.

With the exception noted below, the number of microscopic setae of the metathorax and the pattern they form is identical to that of the mesothorax. Changes in the position of MD1 or the relative positions of the MSD and MV setae of the mesothorax are always exactly repeated on the metathorax. In some *HEPIALIDAE* (*Hepialus*) MD1 of the metathorax is lengthened and probably only functions as a tactile seta, from which it is outwardly indistinguishable. In other *HEPIALIDAE* (*Leto*, *Charagia*) MD1 of both the meso- and metathorax is greatly lengthened. It has already been pointed out that two MD setae are present on the metathorax of all instars of the most, or at least one of the most, highly specialised groups of the Ditrysia, namely the Agrotoidea (*AGROTIDAE*, *ACRONYCTIDAE*, *ARCTIDAE*, *LITHOSIIDAE*, *THAUMETOPOEIDAE*, *LYMANTRIIDAE*, *NOTODONTIDAE*), a superfamily characterised by having an upright egg, a first instar larva with the crochets of the prolegs arranged in a mesoseries (always?) and sometimes having secondary hair, and a specialised obtect pupa.

The *THYATIRIDAE* are sometimes placed near the *GEOMETRIDAE* and sometimes near the *AGROTIDAE*; and it is therefore interesting to note that they lack the additional MD seta of the metathorax, a seta so characteristic of the superfamily Agrotoidea. I have named the most ventral of the two MD setae, MD2, but I have no evidence to show that the new seta is not really the most dorsal. If such evidence is later produced, the most dorsal will have to be named MD2. A glance at Table 4 is sufficient to show that MD2 is a new or recent seta and cannot reasonably be regarded as a primitive seta which has persisted in this group of specialised Lepidoptera but has been lost in all the very much more primitive moths that have been examined.

(2) The abdominal microscopic setae or proprioceptors.

On each side of the first nine segments of the abdomen there are only two setae which unquestionably belong to the system of proprioceptors. One of these, MD1, is opposite D2 or, more rarely, D1, and the other, MV3, is usually opposite a point between V1 and the most mesal seta of the SV group. There can be no doubt that D1 is the homotype of all other setae so named on the abdomen, and the same is true for MV3. There is also little doubt that MD1 is the homotype of MD1 on the meso- and metathorax; and it seems likely that MV3 is the homotype of MV3 of the three thoracic segments. The degree of approximation of these setae to the anterior margin is subject to considerable

variation; and in this respect MV3 varies much more than MD1. In *Hepialus*, for instance, MD1 is close indeed to the anterior margin, but in other species of other families it may be only half-way between the anterior margin and D1. The variation of MV3 in this respect is more striking and often accompanied by a significant change in length. As it moves back from the anterior margin and as it therefore ceases to come so regularly in contact with the segment in front, it appears, if its length is any indication of its function, to function less as a proprioceptor and more as an ordinary tactile organ. An extreme instance of this is seen in *Hepialus* where MV3 is very close to the SV group of tactile setae and as far from the anterior margin as is that group (fig. 18). In some forms

TABLE 4.

The distribution of the microscopic setae on the meso- and metathorax.

	Mesothorax							Metathorax						
	MD1	MD2	MSD1	MSD2	MV1	MV2	MV3	MD1	MD2	MSD1	MSD2	MV1	MV2	MV3
first instar														
PSYCHIDAE (<i>Pumea</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
COSSIDAE (<i>Cossus</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
SESIDAE (<i>Sphecia</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
PIERIDAE (<i>Pieris</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
AGROTIDAE (<i>Hadena</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
ACRONYCTIDAE (<i>Apatele</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
LYMANTRIDAE (<i>Euproctia</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
NOTODONTIDAE (<i>Cerura</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
SPHINGIDAE (<i>Sphinx</i>) .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
mature larva														
ERIOCRANIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
HEPIALIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
INCURVARIIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
ADELIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
TINAEIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
PSYCHIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
COSSIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
SESIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
TORTRICIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
PYRALIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
TYGAENIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
GEOMETRIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
THYATRIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
AGROTIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
ACRONYCTIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
ARCTIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
LITHOSIIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
LYMANTRIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
THAUMETOPOEIDAE .	+	—	+	+	+	+	+	?	?	+	+	+	+	+
NOTODONTIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+
SPHINGIDAE .	+	—	+	+	+	+	+	+	—	+	+	+	+	+

MV3 is found on the proleg, bearing segments far from the anterior margin near or on the basal part of the proleg. In such instances, however, it remains minute; and it is not beyond the bounds of possibility that in these cases it functions as a proprioceptor with respect to the proleg rather than to the segment in front in the same manner as MV2, and possibly also MV3, of the thoracic segments function as proprioceptors for the legs.

In some groups of the Agrotoidea, viz.: *Apatele*, THAUMETOPOEIDAE, and NOTODONTIDAE, two MD setae are present on the first abdominal segment (Table 3). It has already been stated that in the Agrotoidea there are two MD setae on the metathorax. The most ventral of these on both segments is named MD2, and, for reasons already given when discussing the MD setae of the metathorax, there can be little doubt that MD2 of the first abdominal segment

is also a new seta developed comparatively recently in the history of the Lepidoptera. *Apatele alni* L. is peculiar in that two MD setae are present in the first instar, but I have been unable to find more than one on the first abdominal segment of a third instar larva examined. The latter may, however, be abnormal in this respect. Ripley (1923 : 32) has stated that two MD setae are present on the first abdominal segment of *Heliothis armigera* Hübner, but a specimen examined showed no trace of MD2 nor did specimens of *H. dispasea* L. and *H. scutosa* Schiffermüller. The first abdominal segment of some ten genera of the AGROTIDAE (s.str.) was examined and in each MD was unisetose.

(B) *The long or tactile setae.*

Although it is convenient to speak of the long setae as tactile setae, which they undoubtedly are in the vast majority of instances, it is well known that in many of the more recent or specialised groups these setae may become secondarily modified to serve other and quite different purposes. The poison spines of some caterpillars are a case in point.

In number and disposition the tactile setae are considerably more variable than the microscopic setae, but are nevertheless sufficiently constant in these respects to make it possible and useful to give them names and describe their positions and the amount of variation to which they are subject. The tactile setae are undoubtedly the most useful characters, from the point of view of distinguishing species, genera, and even families, that have yet been recognised in the larvae.

The terms primary, subprimary, and secondary are used here in the sense given to them by Fracker. A primary seta is one which I have reason to believe was present in the archetype of the Lepidoptera before the differentiation of the order into suborders took place. It is a seta present in the first and last instars of all but a few specialised families. In some of the specialised families it may be lost after the first moult, or, more rarely, it may be absent in the first instar. For example, in *Pieris* one of the primary setae of the prothorax is absent in the first instar. In other specialised forms, e.g. some LYMANTRIIDAE, the primary setae are no longer distinguishable as such in the first instar larva owing to the fact that already in this instar there appear numerous secondary setae. Sometimes the primary setae may be distinguished in first as well as other instars in spite of the development of numerous secondary setae either because of their different appearance or because the primary setae tend to occur on separate pinnaculæ or sclerotised plates, being associated on such plates with their own group of secondary setae. Each plate and tuft of setae, together known as a *verruca*, is often equivalent to one or at any rate a single group of primary setae. In discussing the variation of the primary and subprimary setae the various ways in which the *verruca* of one setal group fuse with those of another, etc., are omitted. And, in general, no attempt is made here to deal with the setal variations of certain advanced groups of the Ditrysia such as the SATURNIIDAE, BOMBYCIDAE, and related families having a flat egg, the more specialised families of the Agrotoidea, and the whole of the Rhopalocera. I am concerned here with establishing homologies that will apply throughout the order, and the obvious secondary specialisations of the higher Ditrysia throw little light on basic homologies. For descriptions of setal modifications in these higher groups, the papers of Müller (1886), Packard (1890, 1893a, 1893b), Dyar (1894), Fracker (1915), Schierbeek (1917), etc., should be consulted.

Subprimary setae are those which occur throughout the more primitive

families but are nevertheless absent in the first instar. They are further characterised by being few in number and constant in position. The appearance of these setae in later ontogenetic stages is good reason for believing that they have been acquired later in the history of the order than the primary setae. The distinction between primary and subprimary setae is clear enough in most cases, but in a number of fairly primitive diplotremes or Ditrysia a particular seta may be primary in one form and subprimary in another. In *Cossus cossus* L. SV2 is present in the first instar larva on the first and eighth abdominal segments, whereas in *Sphecia bembeciformis* Hübner it is acquired on the first and eighth segments only after the first moult. There is, broadly speaking, a tendency for certain of the setae which are subprimary in all the more generalised families to appear in the first instar of the more highly specialised families. In some of the fairly specialised families, however, one or more of the primary setae may be lost even in the first instar. For instance, SD2 is absent on the metathorax of the first instar larva of *Pieris*. In making distinctions between primary and subprimary setae, the segments on which they are one or the other should be specified. This is particularly true of the SV group of the abdomen, as SV2 may be primary on some segments of one species and not on others of the same species.

In some COSSIDAE (*Cossus*) but not in others (*Zeuzera*) a long tactile seta which is postero-ventrad from SD1 appears after the first moult on the first eight abdominal segments. This seta is not reckoned as a subprimary seta as it does not occur generally in primitive and moderately primitive forms, but appears to be confined to some of the COSSIDAE. I call this a secondary seta, although species which develop secondary setae usually have many such setae. I know of no case analogous to *Cossus* below the Macroheterocera.

Secondary setae are those which have been acquired more recently by the Lepidoptera, possibly in the late Cretaceous or early Eocene. They are additional setae, often very numerous, which occur in nearly all families of the Rhopalocera and in the more specialised members of the different superfamilies of the Macroheterocera. In many of the forms which possess secondary setae in the later instars, such setae are absent in the first instar larva, e.g. *Pieris*. In others, e.g. *Argynnis*, *Euproctis*, and *Cerura*, secondary setae are always present in the first instar larva; and there can be little doubt that such ontogenetic sequences are useful guides in judging the relative antiquity of the various families. For instance, on the recapitulation theory one has little doubt that secondary setae were acquired more recently in the PIERIDAE or the ancestors of the family than in the LYMANTRIIDAE or NOTODONTIDAE where they appear in the first instar. The greater degree of specialisation in the latter two families is also confirmed by the ontogeny of the crochets of the prolegs. In the HESPERIIDAE, PAPILIONIDAE, PIERIDAE, and probably all Rhopalocera, the four ventral pairs of prolegs always have a complete circle of crochets in the first instar. In successive larval instars the outer crochets become smaller and less numerous at each moult until in the mature or nearly mature larva they are lost altogether and only the mesal crochets are strongly developed to form a typical mesoseries. In primitive HESPERIIDAE a complete multi-serial circle is present even in the final instar. In the LYMANTRIIDAE and NOTODONTIDAE, on the other hand, the first instar larva already possesses a well-developed mesoseries and there is in these families no longer any postembryonic evidence that the mesoseries has developed from a complete circle of crochets.

In the following discussion of the primary and subprimary tactile setae, the evidence for the homotypy suggested is briefly reviewed in each case; and the

usual variations as regards the position of the setae on the segments and their relation to adjoining setae are mentioned. As already stated, the fusion and disappearance, or multiplication, of the primary and subprimary setae in the Rhopalocera and more specialised Macroheterocera are ignored.

XD group (Fracker, alpha + gamma; Heinrich, 1a + 1b; Gerasimov, X + IX). This group consists of only two setae, XD1 and XD2, which are confined to the prothorax. Both setae are primary and are present in the first instar of all Lepidoptera, although in a few, e.g. *Cerura*, they may be difficult or impossible to distinguish from the secondary setae. They are very distinct in the first instar of such specialised members of the Rhopalocera as the PIERIDAE and NYMPHALIDAE. A possible explanation of the fact that they have been developed only on the prothorax is given on p. 19, where an account is also given of some recent suggestions that they are the homotypes of some of the proprioceptors of the mesothorax. Both setae are always on or near the anterior margin of the sclerotised plate of the protergum, and XD2 is nearly always directly below XD1. Both are long setae, approximately equal in length, which are always longer than D1 and nearly as long or longer than D2. In some instances the migration of D1 to the anterior margin of the protergal sclerotised plate, e.g. in the HEPIALIDAE, has caused D1 to be considered the homologue of XD1, and XD1 the homologue of XD2. Fortunately, puncture XDc (fig. 23) appears to be invariably associated with XD2, and it will thus serve as an infallible recognition mark. The first seta directly above XD2 is, of course, XD1, which has one puncture, XDa, near its base and another, XDb, more or less between its base and seta D1.

Dorsal group (Dyar & Forbes, ia or i + ib or ii; Fracker, alpha + beta; Gerasimov, I + II). The dorsal group consists of two setae, D1 and D2. Both are primary on all thoracic and abdominal segments and both are distinguishable in all instars except sometimes in those groups which develop numerous secondary setae.

On the abdomen, D1 is always anterior to D2, except sometimes on the ninth segment, where it may be in a vertical row between D2 and SD1; and it is nearly always distinctly shorter than D2. As a general rule, D1 is more dorsal than D2 on the abdomen except on the ninth segment, where D1 is, with few exceptions, ventrad from D2. In the HEPIALIDAE D1 is unusual in that on the ninth segment it is directly anterior to D2 in some genera and antero-dorsad from D2 in other genera. On the eighth segment D1 is, in many Microlepidoptera, more or less opposite D2. In some genera D1 may be more ventral than D2 on the first eight segments. For instance, most of the TINAEIDAE have D1 distinctly more dorsal than D2, as is usual, but in *Scardia* it is D2 which is the more dorsal of the two. In all the higher or very specialised PSYCHIDAE, which feed on flowering plants and have apterous females, D1 is ventral to D2, but amongst the obviously more primitive PSYCHIDAE (often incorrectly placed in the TINAEIDAE) where the larva is carnivorous and the females are not so completely apterous or are even fully winged, D1 is usually directly opposite D2 or distinctly dorsad from the latter. In spite of the fact that in *Eriocrania* D1 is slightly more ventral than D2, it seems likely that the primitive position is with D1 more dorsal than D2. In both the TINAEIDAE and PSYCHIDAE in which the ventral position of D1 relative to D2 is obviously a secondary specialisation, it is interesting to find that on the thoracic segments D1 is always more dorsal than D2. The homotypy of the D setae of the abdomen has never been questioned owing to the characteristic lengths of the two setae and their position relative to the long axis of the body.

On the thoracic segments, D1 and D2 are nearly always close together and usually form a vertical row. Seta D1 was distinctly shorter and more dorsal than D2 in nearly every species examined. On the meso- and metathorax

TABLE 5.

The names of the setae of the thorax and abdomen according to Fracker (1915), Gerasimov (1935), and Hinton.

	Fracker		Gerasimov		Hinton	
	Jugatae	Frenatae	HEPIALIDAE	Others		
Prothorax	Gamma	Alpha	IX	X	Tactile	XD1
"	Epsilon	Gamma	IIIa	IX	"	XD2
"	Alpha	Beta	X	I	"	D1
"	Beta	Delta	I	II	"	D2
"	Rho	Epsilon	II	IIIa	"	SD1
"	Delta	Rho	III	III	"	SD2
"	Eta	Kappa	V	IV	"	L1
"	Kappa	Eta	IV	V	"	L2
"	Theta	Theta	VI	VI	"	L3
"	Pi	Pi	VIIa	VIIa	"	SV1
"	Nu	Nu	VIIIb	VIIIb	"	SV2
"	Sigma	Sigma	VIII	VIII	"	V1
"	—	—	—	Xa	Proprioceptor	MXD1
"	Tau	—	VIIc	VIIc	"	MV2
"	Phi	—	VIIId	VIIId	"	MV3
Meso- and meta-thorax	Alpha	Alpha	I	I	Tactile	D1
"	Beta	Beta	II	II	"	D2
"	Rho	Rho	III	III	"	SD1
"	Delta	Epsilon	IIIa	IIIa	"	SD2
"	Kappa	Kappa	V	IV	"	L1
"	Epsilon	Eta	IV	V	"	L2
"	Theta	Theta	VI	VI	"	L3
"	Pi	Pi	VIIa	VIIa	"	SV1
"	—	Nu	—	—	"	SV2
"	Sigma	Sigma	VIII	VIII	"	V1
"	Gamma	—	Xa	Xa	Proprioceptor	MD1
"	—	—	—	Xb	"	MD2
"	Gamma	—	IXa	IXa	"	MSD1
"	Gamma	—	IXb	IXb	"	MSD2
"	Nu	—	VIIb	VIIb	"	MV1
"	Tau	—	VIIc	VIIc	"	MV2
"	Omega	Omega	VIIId	VIIId	"	MV3
Abdomen, 1-9	Alpha	Alpha	I	I	Tactile	D1
"	Beta	Beta	II	II	"	D2
"	Rho	Rho	III	III	"	SD1
"	Epsilon	Epsilon	IIIa	IIIa	"	SD2
"	Theta	Kappa	IV	IV	"	L1
"	Kappa	Eta	V	V	"	L2
"	Eta	Mu	VI	VI	"	L3
"	Pi	Pi	VIIa	VIIa	"	SV1
"	Nu	Nu	VIIIb	VIIIb	"	SV2
"	Tau	Tau	VIIc	VIIc	"	SV3
"	Sigma	Sigma	VIII	VIII	"	V1
"	—	—	X	Xa	Proprioceptor	MD1
"	—	—	—	Xb	"	MD2
"	Omega	—	VIIId	VIIId	"	MV3

the shorter and more dorsal seta is the homotype of D1 of the abdomen and the longer and more ventral the homotype of D2 of the abdomen. This homotypy is agreed to by all workers. In a few groups the longitudinal arrangement of

D1 and D2 is similar to that of the abdomen. This is the case in the HEPIALIDAE and some species of the genus *Tinaea*, such as *T. walsinghami* Busck. In one species (*Tinaea uterella* Walsingham), D2 is very unusual in being directly in front of D1, from which it is considerably separated. The only evidence of homology in this case is the relative lengths of the two setae.

On the prothorax, D1 and D2 are rarely found in a vertical line, as is usual on the meso- and metathorax. The two setae are, as a general rule, widely separated with D1 antero-dorsad from D2. Very occasionally (e.g. some HEMEROPHILIDAE) D2 is dorsad from D1. The homologies of the D setae of the prothorax have only recently been correctly established by Gerasimov (1935). Fracker (1915), for instance, stated that XD1 was D1, that D1 was D2, and that D2 was a new seta he called delta, which was also found in the HEPIALIDAE on the meso- and metathorax. Fracker's delta of the meso- and metathorax of the HEPIALIDAE is the homologue of his epsilon of other families. The first dorsal seta occasionally migrates to the anterior margin of the protergal sclerotised plate, and in such cases it forms a vertical row with the two XD setae below. This is the condition found in all instars of the HEPIALIDAE and at least in the first instar of the NYMPHALIDAE (*Argynnis selene* Schiffermüller). Seta D1 was correctly identified in the NYMPHALIDAE by Gerasimov (1935, fig. 3), but in the HEPIALIDAE he has (1935, fig. 4) claimed that D1 is the homologue of my XD1 (his X) and D2 is the homologue of D1, as shown in fig. 23.

Subdorsal group (Dyar & Forbes, iii + iiiia; Fracker, rho + epsilon; Gerasimov, III + IIIa). Both of the setae which constitute this group are primary on all thoracic and the first eight abdominal segments, and SD1 (rho or III) is also a primary seta on the ninth abdominal segment from which SD2 (epsilon or IIIa) appears to be invariably absent. Of the two, SD1 is, so far as I am aware, invariably the longer, being usually as long as D2 or L3 except in those groups (HEPIALIDAE, some AGROTIDAE, etc.) where on some segments it is modified and obviously functions as other than a simple tactile receptor. On the abdomen SD1 is typically above the spiracle, but in a few, e.g. nearly all TORTRICIDAE, it is directly anterior to the spiracle on the eighth abdominal segment.

In a number of groups curious structures of unknown function are associated with seta SD1. For example, in the PYRALIDAE there is a pigmented and sclerotised ring around the base of the seta which encloses a fairly large membranous area, and from the basal socket of the seta itself a narrow pigmented bar, which moves when the seta moves, extends under the cuticle to a point beneath the outer pigmented ring. I have shown (1941) that this structure is invariably associated with SD1, although it is sometimes found only on the eighth abdominal segment, or only on the first and eighth segments, or on the mesothorax and the eighth segment. Differences in its distribution are most useful in distinguishing the subfamilies of the PYRALIDAE. In some AGROTIDAE there is a different structure. The socket of SD1 of some segments is very much thickened and unusually darkly pigmented, and the seta itself is unusually slender. This modification of structure in the AGROTIDAE, which is undoubtedly associated with a change in function, is very useful in homologising the setae, as on the prothorax it serves to identify SD1.

On the meso- and metathorax SD1 is directly beneath SD2, and both setae thus form a vertical row which is in line and forms a continuation of the vertical row made by the two dorsal setae. The two subdorsal setae are close together and in a vertical line even in the HEPIALIDAE, where the two dorsal

setae are widely separated and form an oblique line. *Tinaea walsinghami* Busck is very unusual in having the subdorsal setae widely separated and in a horizontal line like the dorsal setae. This species is also exceptional in having SD1 far anterior to SD2. On the prothorax the two setae are widely separated and typically form an oblique or nearly horizontal line with the longer seta antero-dorsad, more rarely antero-ventrad, from the shorter one. The longer and more anterior seta has been considered to be the homotype of SD2 and the shorter and more posterior seta the homotype of SD1 of other segments by Fracker, Forbes, Ripley, Gerasimov, and others. If this is so, it is curious

TABLE 6.

The distribution of the primary tactile setae on the abdomen and meso- and metathorax of first instar larvae of *Fumea casta* Pallas, *Cossus cossus* L., *Sphex bembiciformis* Hübn., *Pieris brassicae* L., *Hadena oleracea* L., *Apatele alni* L., *Cerura vinula* L., and *Sphinx ligustri* L.

	D1	D2	SD1	SD2	Abdomen, 1-9						VI
					L1	L2	L3	SV1	SV2	SV3	
PSYCHIDAE . . .	1-9	1-9	1-9	1-8	1-9	1-9	—	1-9	3-6	—	1-9
COSSIDAE . . .	1-9	1-9	1-9	1-8	1-9	1-9	—	1-9	1-8	—	1-9
SESIIDAE . . .	1-9	1-9	1-9	1-8	1-9	1-9	9	1-9	2-7	—	1-9
PIERIDAE . . .	1-9	1-9	1-9	1-8	1-9	1-8	—	1-9	1-6	—	1-9
AGROTIDAE . . .	1-9	1-9	1-9	1-8	1-9	1-8	—	1-9	2-6	—	1-9
ACRONYCTIDAE . .	1-9	1-9	1-9	1-8	1-9	1-8	—	1-9	2-8	—	1-9
NOTODONTIDAE . .	1-9	1-9	1-9	1-8	1-9	1-8	—	1-9	1-8	1-6 ⁸	1-9
SPHINGIDAE . . .	1-9	1-9	1-9	1-8	1-9	1-8	—	1-9	1-8	1-6	1-9
Meso- and metathorax											
PSYCHIDAE . . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	2-3	—	2-3
COSSIDAE . . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	—	—	2-3
SESIIDAE . . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	—	—	2-3
PIERIDAE . . .	2-3	2-3	2-3	2	2-3	—	—	2-3	—	—	2-3
AGROTIDAE . . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	—	—	2-3
ACRONYCTIDAE . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	—	—	2-3
NOTODONTIDAE . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	2-3	—	2-3
SPHINGIDAE . . .	2-3	2-3	2-3	2-3	2-3	—	—	2-3	2-3	—	2-3

that the length relation of these two setae is the reverse of that of all other segments on which both are found. This might be explained on the grounds that as the shorter seta (SD2) migrates towards the anterior margin the same need to protect the neck and base of the head, which probably accounts for the development of the two XD setae, has also caused, through selection, a lengthening of SD2. As against this homology, however, the following facts may be cited:—

(1) In the AGROTIDAE (*Hadena*, etc.) the seta with the modified socket is certainly SD1, and it is often considerably antero-ventrad from, or even directly anterior to, the normal seta, which is SD2.

(2) When two tactile setae greatly alter their position in respect to each other, they usually maintain their length relation. This is generally true of the cranial setae as well as those of the thorax and abdomen.

⁸ Secondary setae associated with these in first instar larvae.

(3) In the *HEPIALIDAE*, D1 has migrated to a position near the anterior margin of the protergal sclerotised plate and is in line with the two XD setae, but it is nevertheless distinctly shorter than either.

As so many of the arguments for the homology of the setae have been based on the setae of the *HEPIALIDAE*, it is worth discussing the prothorax of this family in some detail, particularly as certain obviously secondary specialisations it possesses have been considered to represent the primitive setal pattern of the *Lepidoptera*. The puncture I have called XDc (fig. 23) has been found near the base of XD2 in all the *Lepidoptera* I have seen. This puncture thus serves to establish with certainty the identity of XD2 in those species which have an atypical setal distribution. Fracker and Gerasimov have not used puncture XDc as a means of identifying seta XD2, and have thus come to believe that in the *HEPIALIDAE* this seta is the homotype of SD2 of other segments and homologous to SD2 of the prothorax of larvae of other families. In other words, their epsilon or IIIa, as the case may be, is in reality homologous to XD2 in the *HEPIALIDAE*, but in all other families it is homologous to SD1. The long seta immediately above XD2 must be XD1, so that the shorter seta above XD1 (fig. 23) is obviously D1, which is more dorsal and considerably more anterior than D2. Slightly behind and on either side of XD1 are nearly always two punctures. These punctures are often arranged in a line behind XD1 and between it and D1. In the *HEPIALIDAE* the punctures again lie more or less between the two setae considered to be XD1 and D1, and thus afford further evidence for the homologies suggested here. Puncture XDa is always close to the base of XD1, but puncture XDb is usually half-way between XD1 and D1. It will be noticed that Fracker was correct in calling D1 alpha, but his alpha of other families is homologous to his gamma of the *HEPIALIDAE* (Table 5).

The more ventral of the subdorsal setae is long and very slender and has a heavily pigmented area around its base, two modifications very similar or essentially identical to those of SD1 of many *AGROTIDAE*. The modified ventral seta is in the same position as that of some *AGROTIDAE*, and there can be little doubt that it is SD1. It therefore follows that the seta immediately above it must be SD2. Thus in the *HEPIALIDAE* the SD group is similar in position and morphological modifications to the same group in some *AGROTIDAE*—chiefly those with partly subterranean habits. The seta above SD2, which is also modified like SD1, is D2. This has been established by elimination and is supported by the position of D2, which is only slightly more ventral than in other families where its identity is not in question. In some *HEPIALIDAE*, e.g. *Charagia*, D2, SD1, and SD2 arise from a large, oval, densely pubescent depression. Fracker has correctly identified D2 as beta, but in other families, for reasons best known to himself, he calls the same seta delta. Gerasimov considered that D2 of the *HEPIALIDAE* was homologous to D1 of other families, and he named it "I" in the *HEPIALIDAE*.

On the first eight abdominal segments of some groups of the *Monotrysia* (*HEPIALIDAE*) and *Microlepidoptera* (some *TINAEIDAE*, some *PYRALIDAE*, etc.) SD2 is a fairly long tactile seta more or less dorsal to SD1, as it is on the meso- and metathorax; and both Fracker and Gerasimov have regarded it as the homotype of SD2 of the thoracic segments. This homotype is accepted as correct in this paper although a number of facts suggest that the abdominal seta I have called SD2 is not the homotype of the thoracic SD2. As already stated, SD2 appears to be invariably absent on the ninth abdominal segment, whereas SD1 is here always present. There are some grounds for believing

that SD2 of the abdomen is one of the position receptors occasionally modified to become an ordinary tactile receptor. In discussing the distribution of the proprioceptors it was shown that both MD1 and MV3 occasionally become long and in all outward parts they are then indistinguishable from tactile setae. This morphological similarity implies a functional similarity. That a proprioceptor can become a tactile receptor appears to be indisputable, but the converse has not yet been proven.

In the majority of groups, including the ERIOCRANIIDAE, Monotrysis, and many of the more primitive Ditryisia, SD2 is a minute seta which, as regards size, would appear to belong to the system of proprioceptors. When SD2 is microscopic, it is typically anterior to, or antero-dorsal from, the spiracle. The spiracles of the abdomen are usually on the middle or anterior half of the segments on which they occur, and each is likely to be partly or entirely covered by the segment in front when, as sometimes happens, the larva turns sharply sideways. It is, therefore, possible that the function of SD2 in those larvae where it is minute is chiefly to detect the segment in front and so enable the larva to prevent the spiracle from being rendered more or less useless by being covered.

In all first instar larvae examined, SD2 of the abdomen was microscopic, whereas SD2 of the thorax was relatively as long as in later instars. Unfortunately, no first instar larvae are available of species which have a long SD2 in later instars. But the appearance of SD2 of the abdomen as a microscopic seta in the first postembryonic ontogenetic stage of fairly primitive forms, such as *Cossus* and *Sphecia*, suggests that SD2 might have originated as one of the microscopic setae and is, in point of fact, the homotype of one of the MSD setae of the two posterior thoracic segments. If SD2 originated as a tactile seta which in some species subsequently changes structure and function to become a proprioceptor, one has here a case the converse of which has already been shown to be possible. As in the most primitive Lepidoptera (ERIOCRANIIDAE) the proprioceptor and tactile receptor systems are already sharply differentiated, the question of whether the proprioceptor system arose in the first place as such, or whether it arose by modification of some of the already existing tactile setae, must be left unanswered pending an investigation of the setae in more primitive orders such as the Mecoptera.

The minute size of SD2 in the majority of larvae has resulted in its being fairly generally overlooked by most workers, including myself (1941), in spite of the fact that as long ago as 1904 Bacot stated that its occurrence was nearly universal. Its minute size has also made possible a number of incorrect homologies. For instance, in the THYATIRIDAE and COSSIDAE Fracker has mistaken a secondary seta for SD1 (rho) and has thus named the seta which is really SD1 epsilon, the second subdorsal being minute and in front of the spiracle in both of these families. In the ARCTIIDAE and in the AGROTIDAE with setal tufts or verrucae, Fracker has overlooked SD2 and he thus believed that the verruca which represents only SD1 is homologous to SD1 plus SD2.

Lateral group (Dyar & Quail & Forbes: iv + v + vi. Fracker: kappa + eta + mu on the abdomen; kappa + eta + theta on the thorax of all and the abdomen of the HEPIALIDAE. Garman & Gerasimov, IV + V + VI). Of the three setae which constitute the L group, L1 is nearly always the longest on the thoracic segments and L2 the next longest. On the abdomen, on the other hand, it is almost invariably L3 which is the longest and L1 is usually the next longest, but L1 and L2 are very often subequal in length. That the three lateral setae of the abdomen are the homotypes of the three lateral setae of the thorax has

been admitted by nearly all workers, although there is some difference of opinion as to the homotypy of the components of the lateral groups of the thorax and abdomen.

Fracker's opinion of the homotypy of the lateral group of the thorax and abdomen departs widely from those of other workers. Fracker believes that the *HEPIALIDAE* differ from all other families in that L3 (μ) is absent on the abdomen and that the most dorsal seta of the lateral group is acquired after the first moult and is a new seta he calls theta. In *Hepialus* L1 and L2 are caudad from the spiracle on the first eight abdominal segments and both are more dorsal than is usual. In the second instar, seta L3 appears for the first time, and L1 and L2 migrate farther dorsally, so that L2 now appears in the usual position of L1, and L3 is slightly below the usual position of L2. Fracker thus interpreted L3 as L2 and L2 as L1, so that he arrived at the conclusion that the most dorsal of the three (in reality L1) appeared for the first time after the first moult. One result of this was that he believed he had discovered a most striking difference between the *Jugatae* and *Frenatae*, viz.: in the *HEPIALIDAE* theta (dorsad from kappa and eta) appeared in the second instar, whereas in the higher *Lepidoptera* a seta not homotypic with theta, i.e. μ (ventrad from kappa and eta), appeared in the second instar.

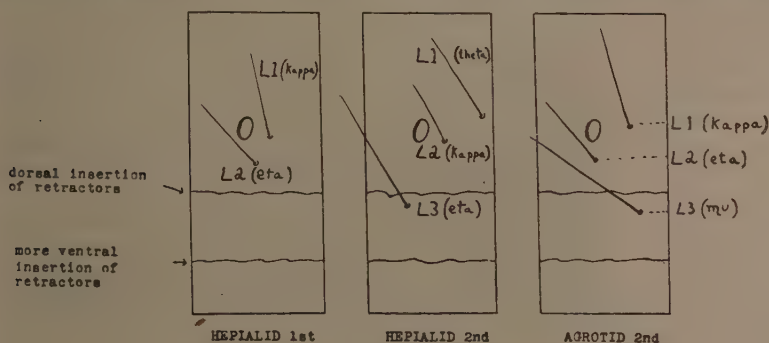
Forbes (1916) showed that in the "*Frenatae*" the subprimary seta L3 (μ or VI) is always below the subventral fold on proleg bearing segments, i.e. below the fold caused by the dorsal insertion of the retractors of the proleg and above the fold caused by the second and more ventral insertion of the retractors. In the second and later instars of the *HEPIALIDAE* there is a seta between the two folds just mentioned, and this seta (eta of Fracker) is undoubtedly homologous to Fracker's μ of the "*Frenatae*." Fig. 24 clearly shows that Fracker's homologies of the lateral setae of the *HEPIALIDAE* cannot be accepted. It is interesting to note that in the *ERIOCRANIIDAE* (fig. 17) L1 is relatively much nearer the medio-dorsal line than it is in the *HEPIALIDAE*.

The first and second lateral setae are primary on the first eight abdominal segments, and they are, with the exception of some of the most specialised *Macroheterocera* which develop setal tufts, always present in the first instar (Table 6). Their position in respect to each other and to the spiracle is of considerable use in distinguishing genera and families. In many groups they are close together, often on the same pinnaculum, whereas in others they are widely separated; and there appear to be but few families which represent an intermediate condition between these two extremes. The first lateral seta is often behind the second and usually slightly more dorsal than the latter, but it is sometimes antero-ventrad from the second. The third sublateral seta is subprimary. It is always present some distance below L2 after the first moult.

On the ninth abdominal segment the lateral group is arranged in a more or less vertical line, and it is therefore very difficult to name the components of the group. As a general rule, the relative lengths of the setae are the best guide in naming them. Table 6 shows the distribution of the setae of the ninth segment in a few families. The distinction between primary and subprimary lateral setae is no longer clear on the ninth segment. For instance, a fairly primitive diplotreme, *Sphecia*, has all three L setae present in the first instar, while in the first instar of other primitive *Ditrysia*, *Fumea* and *Cossus*, only L1 and L2 are present. In the *PIERIDAE*, *AGROTIDAE*, *ACRONYCTIDAE*, *NOTODONTIDAE*, and *SPHINGIDAE* only one lateral seta is present on the ninth, presumably L1. In the first instar of the *SESIIDAE* and in the mature larva

of the PYRALIDAE, TORTRICIDAE, and others, where all three lateral setae are present, the most dorsal (L2) is short, below it there is a long seta (L1), and below the latter another seta (L3) which may be only slightly shorter but is rarely as short as L2.

On the meso- and metathorax (Table 6) L1 is invariably primary and L2 and L3 always subprimary. On these thoracic segments they are nearly always so arranged that L3 is postero-dorsad from L1 and L2 is antero-dorsad from L1. In the HEPIALIDAE (fig. 21), however, L2 is antero-dorsad from L1, and in the ERIOCRANIIDAE (fig. 20) L3 is antero-dorsad from L1. In the HEPIALIDAE Gerasimov (1935, fig. 4) has suggested a homotypy for the three lateral setae with which I cannot agree. In terms of my own nomenclature, his L1 (IV) is my L2 and his L2 (V) is my L1. On the prothorax L1 and L2 are primary. In all the Ditrysia which have the seventh segment of the male pupa movable, as well as in a few which have it fused to the eighth, L3 appears after the first moult. It is easily recognised, as it is a short seta which is nearer to the spiracle



24

FIG. 24.—Homologies of the lateral group of setae of the third abdominal segment in the HEPIALIDAE and higher Lepidoptera.

than L1 and L2. The homotypy of the lateral setae of the meso- and metathorax suggested here is based chiefly on a comparison of the lateral setae of the prothorax. The long primary seta is very unlikely to be the homotype of L3 of the abdomen, as the latter is invariably subprimary. The choice lies between L1 and L2; and of these L1 is the more likely because of the two it is the best-developed seta on the abdomen and because on the prothorax, where both L1 and L2 are primary as on the abdomen, L1 is a very long seta and L2 considerably shorter. This length relation on the prothorax is only maintained on the meso- and metathorax if it is assumed that the primary seta of these segments is L1. On the prothorax of species which possess L3 after the first moult, it is usual to find L3 some distance behind L1 and L2, which are usually closer to each other than either is to L3. By analogy, therefore, the most posterior seta of the meso- and metathorax is probably L3. Gerasimov (1935) also considered that the most posterior seta of these segments was L3.

Subventral group (Quail & Forbes, VII; Dyar & Garman, VII on abdomen and VI on the thorax; Fracker, $\pi + \nu + \tau$; Gerasimov, VIIa + VIIb + VIIc + VIId). Of the three setae which comprise the subventral group,

never more than two, SV1 and SV2, are present in the first instar larva of the monotremes and all but the most specialised diplotremes. Two subventral setae are universally present on the prothorax of the first instar, and their number is never increased in the second or later instars except in those highly specialised Ditrysia which develop secondary setae. The meso- and metathorax of the first and later instars are identical as regards the number of SV setae they possess. In species which do not develop secondary setae, one or two setae, never more than two, are present in first and later instars; and their number is apparently neither increased nor diminished in different instars.

It seems almost certain that two SV setae can be regarded as the primitive number on the two posterior thoracic segments. Unfortunately, no first instar larvae of the Daconypha are available, but, by analogy with what occurs in other larvae, there is little doubt that these segments will be found to have two SV setae in the first instar since two are present in later instars. Two SV setae are of fairly general occurrence amongst the monotremes, and two occur on the most primitive Ditrysia which are available, *i.e.* all PSYCHIDAE and most TINAIDAE. It is true that the first and later instars of the HEPIALIDAE have only one SV seta, but this family is in few particulars as primitive as the ERIOCRANIDAE, and it has already been shown that its larvae, like its pupae, are highly specialised in a surprising number of directions. It is interesting to note that two SV setae occur on the meso- and metathorax of the first instar of the SPHINGIDAE (*Sphinx*) and NOTODONTIDAE (*Cerura*), but I am inclined to think that the second of these setae has been evolved *de novo*, Dollo's law notwithstanding.

The SV setae of the prothorax appear to be always in a horizontal line. When there are two SV setae on the meso- and metathorax, they may be arranged in a horizontal or vertical line, and differences of this sort have been found to be very useful in distinguishing groups of genera in some families, *e.g.* the TINAIDAE.

On the abdominal segments which have ventral prolegs (3-6) there are always two SV setae in the first instar and three in the second, again excepting specialised diplotremes with secondary setae. In the first instar of the SPHINGIDAE (*Sphinx*) there are three, one of which is near the outer base of the proleg and considerably separated from the other two, which are close together near the apex. It is difficult to say whether this additional seta is the homologue of SV3 or whether it is a secondary seta. In descriptive work it is important to distinguish between the components of the SV group. The long primary seta is SV1, and the shorter seta, which is usually antero-mesad from it, is SV2. At the first moult a third seta appears laterad (dorsad) or antero-laterad from SV1, and this is the subprimary SV3. The third subventral is occasionally antero-mesad from SV1, but it is never as mesad as SV2. This subprimary seta is always distinctly shorter than SV1 and often shorter than SV2.

On the first two abdominal segments of *Eriocrania*, the aculeates *Incurvaria* and *Adela*, and many of the most primitive non-aculeates there are two SV setae in later instars, SV2 being very much shorter than SV1. In the most primitive first instar larva available, *Fumea*, only SV1 is present. In the first instar of the SESIIDAE, AGROTIDAE, and ACRONYCTINAE only SV1 is present on the first segment but both SV1 and SV2 are present on the second segment. In the COSSIDAE, PIERIDAE, and SPHINGIDAE SV1 and SV2 are present on both the first and second abdominal segments. From the facts just cited it is clear that SV3 is not only never present in the first instar of primitive and even such specialised forms as the PIERIDAE and AGROTIDAE, but also that in many of the

most primitive Lepidoptera it is not developed even in later instars. In some of the most primitive Ditrysia, e.g. the *TINAEIDAE*, SV3 is present in the second instar. As SV3 is present in the later instars of the *HEPIALIDAE*, the conclusion may be justified that it has here been acquired independently. Because of insufficient material it is not possible to say at this time at what point above the branching off of the *HEPIALIDAE* from the remainder of the Monotrysia and all the Ditrysia SV3 was acquired in later instars. The second subventral may, on examination of more material of the primitive forms, prove to be absent in the most primitive on both the first and second abdominal segments of the first instar larvae.

The occurrence of the subventral group on the seventh and eighth abdominal segments of first instar larvae is shown in Table 6. As in the case of the first two segments, SV1 is always present, SV2 is often absent on both but more often on the eighth (also in mature larvae), and SV3 is always absent. Seta SV3 is absent even in the later instars of the majority of the Lepidoptera examined. In short, as regards the first and second and seventh and eighth abdominal segments, whereas SV1 is always a primary seta, SV3 does not quite fit into the category of setae previously defined as subprimary but can almost be regarded as a secondary seta, and still less does SV2 fit into one of these categories. The latter is neither clearly a primary nor a subprimary in the sense in which these terms are used by Fracker (1915) and generally throughout this paper.

On the ninth abdominal segment of first instar larvae, excepting some of those with secondary setae, SV1 is always present and SV2 and SV3 always absent. In later instars SV2 is nearly always absent, and no larvae have been seen with SV3.

Ventral group (Dyar & Forbes & Gerasimov, VIII; Fracker, sigma). In the first as well as later instar larvae of all Lepidoptera examined, there is a seta near the medio-ventral line of all thoracic and abdominal segments. This seta, V1, is always nearer the medio-ventral line than any of the subventral group, and, as it is nearly always widely separated from the most mesad of the SV group, it is easily distinguishable. The ventral group is always unisetose except, of course, in the Rhopalocera and Macroheterocera which develop secondary setae. On the proleg bearing segments, V1 is often found on the mesal side of the proleg itself. On the thorax of the case-bearing *ADELIDAE* and *PSYCHIDAE*, and also in many, but not all, of the case-bearing *TINAEIDAE*, V1 is on the coxa; and this is so even in some *TINAEIDAE* with relatively small coxae which do not meet on the medio-ventral line.

ACKNOWLEDGMENTS.

My best thanks are due to Mr. W. H. T. Tams, who has helped me in many different ways during the course of this work and who generously lent me his collection of reprints on lepidopterous larvae and made available to me blown larvae of several hundred species. I am also indebted to Mr. J. F. Gates Clark, Dr. F. van Emden, Dr. J. W. Evans, Dr. O. W. Richards, Mr. J. A. Downes, and Dr. F. Zeuner for their aid on some of the problems encountered, and to Mr. E. W. Classey for a larva of *Heliothis armigera* Hübner.

REFERENCES.

- BACOT, A., 1904, [No title]. *Entomologist* 37 : 94.
- BÖRNER, C., 1939, Die Grundlagen meines Lepidopterensystems. *Verh. VII. Int. Congr. Ent.* 1938, 2 : 1372-1424, 51 figs.
- BUSCK, A., 1914, On the classification of the Microlepidoptera. *Proc. ent. Soc. Wash.* 16 : 46-54, 1 pl.
- , 1932, On the female genitalia of the Microlepidoptera and their importance in the classification and determination of these moths. *Bull. Brooklyn ent. Soc.* 26 : 199-211, 5 pls. (1931).
- CHAPMAN, T. A., 1913, Some Lycaenid notes, with a discussion of the segmentation of the abdomen in Lepidoptera. *Trans. City Lond. ent. nat. Hist. Soc.* 22-23 : 67-74, 7 pls.
- , 1917, *Micropteryx* entitled to ordinal rank. Order Zeugloptera. *Trans. ent. Soc. Lond.* 1916 : 310-14, 12 pls.
- CRUMB, S. E., 1934, A classification of some Noctuid larvae of the subfamily HYPENINAE. *Ent. Amer.* 14 : 133-96, 7 pls.
- DAMPE, A., 1910, Zur Kenntnis gehäusetragender Lepidopterenlarven. *Zool. Jb. (Suppl.)* 12 : 513-608, 54 figs.
- DYAR, H. G., 1894, A classification of lepidopterous larvae. *Ann. N.Y. Acad. Sci.* 8 : 194-232, 5 figs.
- , 1896, Note on the head setae of lepidopterous larvae, with special reference to the appendages of *Perophora melsheimerii*. *J. N.Y. ent. Soc.* 4 : 92-3, 2 figs.
- FORBES, W. T. M., 1910, A structural study of some caterpillars. *Ann. ent. Soc. Amer.* 3 : 94-143, 143 figs.
- , 1916, On certain caterpillar homologies. *J. N.Y. ent. Soc.* 24 : 137-42, 1 fig.
- , 1923, The Lepidoptera of New York and neighbouring States. *Mem. Cornell Univ. agric. Exp. Sta.* 68 : 729 pp., 439 figs.
- FRACKER, S. B., 1915, The classification of lepidopterous larvae. *Illinois biol. Monogr.* 2 : 169 pp., 112 figs.
- GARMAN, H., 1921, Some neglected setae of lepidopterous larvae. *Ann. ent. Soc. Amer.* 14 : 145-9, 5 figs.
- GERASIMOV, A. M., 1935, Zur Frage der Homodynamie der Borsten von Schmetterlingsraupen. *Zool. Anz.* 112 : 177-94, 8 figs.
- GRANDI, G., 1933, Morfologia ed etologia comparata di insetti a regime specializzato. IV. La morfologia comparata di vari stati larvali di 30 Microlepidotteri minatori appartenenti a 15 generi ed a 11 famiglie. *Boll. Lab. Ent., Bologna* 5 : 143-307, 129 figs.
- HEINRICH, C., 1916, On the taxonomic value of some larval characters in the Lepidoptera. *Proc. ent. Soc. Wash.* 18 : 154-64, 5 figs.
- , 1918, On the lepidopterous genus *Opostega* and its larval affinities. *Proc. ent. Soc. Wash.* 20 : 27-38, 34 figs.
- , 1921, Some Lepidoptera likely to be confused with the pink bollworm. *J. agric. Res.* 20 : 807-36, 17 pls.
- HINTON, H. E., 1941, The larvae of the Lepidoptera associated with stored products. *Bull. ent. Res.* 34 : 163-212, 128 figs.
- MOSHER, E., 1916, A classification of the Lepidoptera based on characters of the pupa. *Bull. Illinois St. Lab. nat. Hist.* 12 : 17-159, 116 figs.
- MÜLLER, W., 1886, Südamerikanischer Nymphalidenraupen. Versuch eines Natürlichen Systems der Nymphaliden. *Zool. Jb. (Syst.)* 1 : 417-678, 4 pls.
- PACKARD, A. S., 1890, Notes on some points in the external structure and phylogeny of lepidopterous larvae. *Proc. Boston Soc. nat. Hist.* 25 : 83-114, 2 pls.
- , 1893a, The life history of certain moths of the family COCHLIOPODIDAE, with notes on their spines and tubercles. *Proc. Amer. phil. Soc.* 31 : 83-108, 4 pls.

- PACKARD, A. S., 1893b, Studies on the transformations of moths of the family SATURNIDAE. *Proc. Amer. Acad. Arts Sci.* **23** : 55-92, 10 figs.
- , 1895, On a new classification of the Lepidoptera. *Amer. Nat.* **1895** : 636-47; 788-803, 15 figs.
- QUAIL, A., 1904, On the tubercles of thorax and abdomen in first larval stage of Lepidoptera. *Entomologist* **37** : 269-72, 1 pl.
- RIPLEY, L. B., 1923, The external morphology and postembryology of Noctuid larvae. *Illinois biol. Monogr.* **8** : 169 pp., 61 figs.
- SCHIERBEEK, A., 1917, *On the setal pattern of caterpillars and pupae.* ii + 157 pp., 5 pls. Leiden.
- SNODGRASS, R. E., 1928, Morphology and evolution of the insect head and its appendages. *Smithson. misc. Coll.* **81** (3) : 158 pp.
- , 1935, *Principles of insect morphology.* London.
- TILLYARD, R. J., 1919, On the morphology and systematic position of the family MICROPTERYGIDAE (*sens. lat.*). *Proc. linn. Soc. N.S. Wales* **44** : 95-136, 1 pl., 14 figs.
- , 1923a, On the larva and pupa of the genus *Sabatinca* (Order Lepidoptera, family MICROPTERYGIDAE). *Trans. ent. Soc. Lond.* **1922** : 437-53, 1 pl., 4 figs.
- , 1923b, On the mouth-parts of the MICROPTERYGIDAE (Order Lepidoptera). *Trans. ent. Soc. Lond.* **1923** : 181-206, 12 figs.
- TSOU, T. H., 1914, Homology of the body setae of some lepidopterous larvae. *Trans. Amer. micr. Soc.* **33** : 223-60, 4 pls.
- ZEUNER, F. E., 1946, *Dating the past.* 422 pp., 24 pls. London.

Vol. 97. Part 2. Pp. 39-54, 3 figs.

22nd July, 1946.

IMP. INST. ENT.

— LIBRA

13 AUG 1946

SERIAL
SEPARATE

Eu. 344

THE

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

✓ EVANS, J. W., M.A., D.Sc. A natural classification
of leaf-hoppers (Homoptera, Jassoidea). Part 2:

AETALIONIDAE, HYLICIDAE, EURYMELIDAE. . 39-54, 3 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 5s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.
C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.
H. B. WILLIAMS, LL.D.

A. WELT, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,
D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Registrar :

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. **British National Committee for Biology** (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. **Local Committee of Management of Wicken Fen.**

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. **National Trust for Places of Historic Interest or Natural Beauty.**

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. **New Forest Association.**

Mr. W. Fassnidge, appointed 1934.

5. **New Forest Joint Committee.**

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. **Royal Meteorological Society. Phenological Committee.**

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. **Biology War Committee.**

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. **Council for the Promotion of Field Studies.**

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. **Joint Bioclimatic Committee.**

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

A NATURAL CLASSIFICATION OF LEAF-HOPPERS (HOMOPTERA, JASSOIDEA).

PART 2: AETALIONIDAE, HYLICIDAE, EURYMELIDAE

By J. W. EVANS, M.A., D.Sc.

(Imperial Institute of Entomology.)

Manuscript received 19th October, 1945.

(Read 16th January, 1946.)

WITH THREE TEXT-FIGURES.

IN Part 1 of this series (Evans, 1946) the Jassoidea were divided into five families: the AETHALIONIDAE (more correctly the AETALIONIDAE), MEMBRACIDAE, HYLICIDAE, EURYMELIDAE and JASSIDAE.

The three families dealt with in the present part, though in many respects the most interesting of all the Jassoidea, are the least known, since all have a limited geographical distribution.

No attempt will be made in this, or in any other part, to present a critical revision of the groups under consideration, although several are in need of such treatment. The purpose of this series of papers is to illustrate the principal diagnostic features of every natural group of leaf-hoppers (apart from the MEMBRACIDAE); to describe, in concise terms, the salient features of their structure, general appearance, biology and distribution; to assign as many genera as possible to their correct position in the system of classification presented and to discuss the position of each division within the Jassoidea.

AETALIONIDAE (fig. 1).

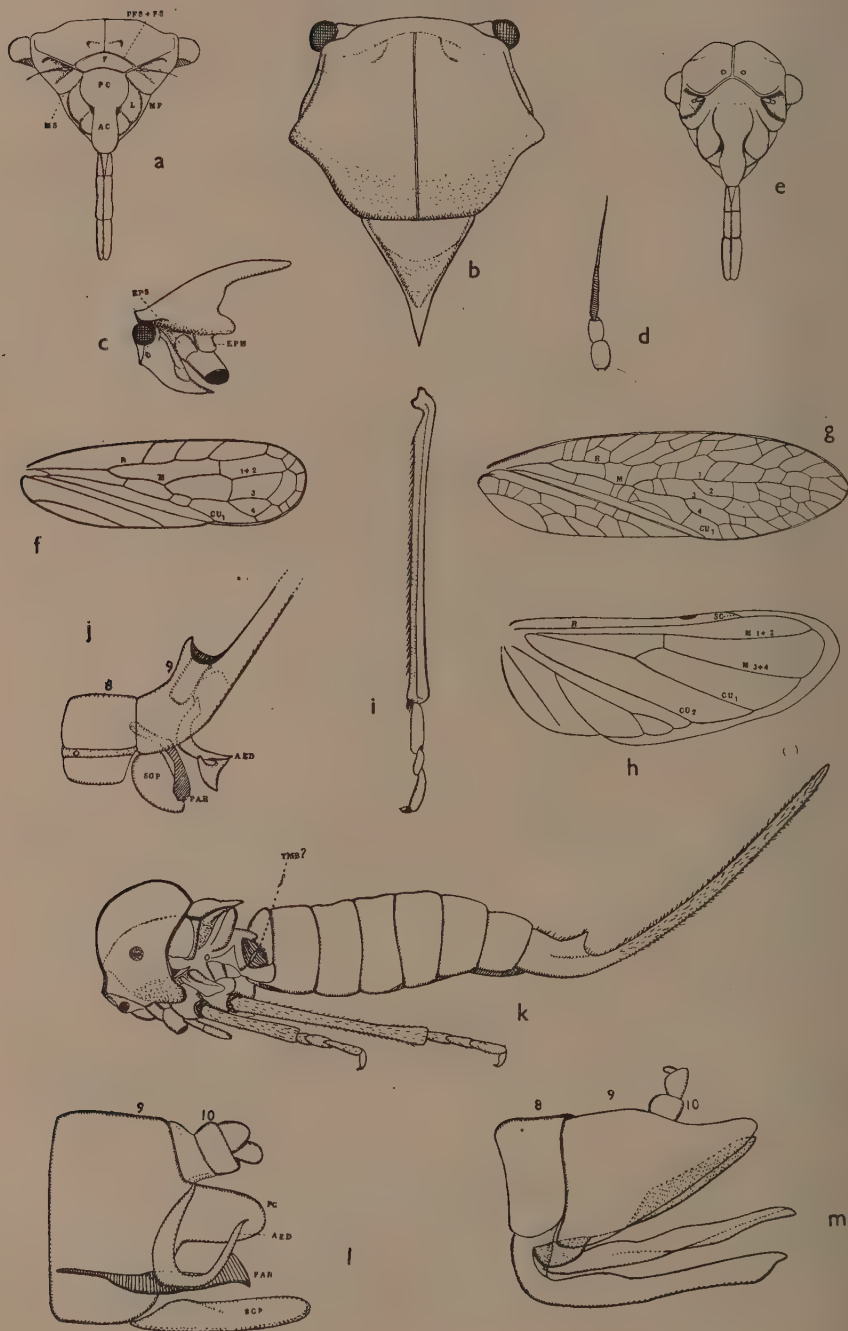
The family AETALIONIDAE comprises two genera, *Aetalion* Latreille and *Darthula* Kirkaldy. *Aetalion* has sometimes been considered a membracid genus (Stål, 1869; Fowler, 1897; Goding, 1925, 1927, 1931) and sometimes a jassid genus (Ashmead, 1889; Evans, 1939). The relationship of *Darthula* to *Aetalion* is undoubted and has received general acceptance (Stål, 1869; Distant, 1907; Haupt, 1929; China, 1941). The two genera, however, are sufficiently distinct to be placed in separate sub-families, the AETALIONINAE and the DARTHULINAE.

Distribution.

Species in the genus *Aetalion* are confined to Central America and tropical South America. *Darthula hardwickii* Gray, the sole representative of the genus, has been recorded from Sikkim, Assam, Burma and Western Yunnan.

Size, Coloration and General Appearance.

Aetalion spp. range in size from 5 to 15 mm. and are reddish or yellowish-brown in colour. *D. hardwickii* has a total length of 28 mm., of which the apical 12 mm. consists of the prolonged ninth abdominal segment. It is brown in colour, and living specimens have been described as having scarlet thighs and as being covered with a white, waxy bloom (Colthurst, 1931).



Food-plants.

Aetalion reticulatum L. is polyphagous and feeds on a wide range of cultivated and indigenous trees and shrubs.

Habits.

Both the adults and the nymphs are gregarious and are attended by ants. The eggs of *Aetalion* are laid on the branches of the food-plant and are contained in raised oothecae formed from the product of the glands of the female (Marques, 1928). Colthurst records *Darthula* as depositing "a concentric, brilliantly scarlet and beady cluster of eggs between herself and the branch on which she rests." Also, that after oviposition, the female dies and her dried body serves to give protective cover for the eggs.

Description.

Head. The proximal segment of the labium is long and exposed. The ante-clypeus is not separated from the post-clypeus by a transverse suture and the post-clypeus is small and not enlarged posteriorly. Traces remain of an epistomal suture, separating the frons from the post-clypeus, and the frons is a distinct sclerite. The post-frontal and frontal sutures form a continuous line at the back of the frons, and the inwardly-directed lines which form the lateral margins of the frons in fig. 1, a, are not the frontal sutures but the bases of the antennal ledges. The lora are large and swollen and are bounded, in part, posteriorly by the maxillary suture. This suture marks the original position of the sides of the anterior margin of the head capsule. The maxillary plates are narrow and almost completely concealed by the lora. The antennae are short, the antennal ledges prominent and backwardly directed, and the antennal depressions deep. The ocelli lie close to each other on either side of the coronal suture. The eyes are small but prominent and there is but little development of a crown.

Thorax. The pronotum, which has a median longitudinal ridge, is large and declivous and wide laterally. The pro-episterna are exposed and not partially concealed by the head. The scutellum is long, narrow and raised and both the pronotum and scutellum are pitted and rugose. The paired sternal invaginations are separate in the pro- and mesothorax but fused together in the metathorax.

Legs. The fore and middle femora are wide and cylindrical and the hind femora are short and cylindrical. The hind tibiae are long, quadrilateral in section and may have one row of small spines. The hind coxae, which are rounded, do not extend laterally as far as the ventral margin of the thorax.

Tegmina. The veins are raised in relief and the venation is reticulate to a varying degree. The radius is unbranched, the media has three or four branches and the first cubitus is apparently unbranched. There is considerable variation in minor details of venation, not only between different individuals, but often between the two tegmina of the same insect.

FIG. 1.—a. *Aetalion reticulatum*, head; b. *A. reticulatum*, head and thorax, dorsal aspect; c. *A. reticulatum*, head and thorax, lateral aspect; d. *A. reticulatum*, antenna; e. *Darthula hardwickii*, head; f. *Aetalion viticolle*, tegmen; g. *D. hardwickii*, tegmen; h. *D. hardwickii*, wing; i. *A. reticulatum*, hind tibia and tarsus; j. *D. hardwickii*, male genitalia; k. *D. hardwickii*; l. *A. viticolle*, male genitalia; m. *A. reticulatum*, female genitalia.

Abbreviations.

AC., anteclypeus; AED., aedeagus; EPM., epimeron; EPS., episternum; F., frons; FS., frontal suture; L., lorum; MP., maxillary plate; MS., maxillary suture; PAR., paramere; PC., postclypeus; PFS., postfrontal suture; PG., pygophore; SGP., subgenital plate; TMB., tymbal.

Wings. The radius is unbranched; otherwise the wing has normal jassid venation.

Abdomen. There is a raised ridged boss on each side of the first abdominal tergite. These bosses are best developed in *Darthula hardwickii*, especially in the male, but also occur in *Aetalion* spp.

Male Genitalia. The sub-genital plates are fused together proximally; the aedeagus of *Aetalion viticollis* Stål is hook-shaped and the base of the hook rests in a depression formed by the apposed parameres. The pygophores of *Aetalion* are short, but in *Darthula* the tergites of the ninth segment are enormously prolonged, in both sexes, and form a tubular structure. The basal plate is small, and the aedeagus, as well as being in contact with the basal plate, is in contact with the base of the anal segment.

Female Genitalia. The first and second valvifers are irregular in outline and are not serrated. The anal segments are large and prominent.

Discussion.

In their manner of oviposition the AETALIONIDAE differ from the rest of the Auchenorrhyncha, with the exception of certain fulgoroids, since they lay exposed eggs, or eggs in raised oothecae, and do not insert them into plant tissue. Their gregarious and sessile habits and their association with ants are characteristics which they share with the MEMBRACIDAE and EURYMELIDAE.

The head exhibits a combination of several primitive features, notably the undivided clypeus, the distinct frons and the retention of the maxillary sutures. The hypothesis that the lora are lateral lobes of the clypeus and not extensions of the hypopharynx receives support from the structure of the head of *Darthula*. The position of the ocelli alone affords evidence of secondary specialisation. Both Stål and Distant placed *Aetalion* at the end of the CENTROTINAE (MEMBRACIDAE) and the resemblance of the heads of species comprised in this subfamily with those of the AETALIONIDAE is evidence of relationship between the two groups. Nevertheless, in having small lora, wider maxillary plates and a transverse suture between the ante- and postclypeus, the membracids have acquired characters which render them quite distinct from the aetalionids.

The large prothorax is another character shared with membracids, but again in the shape of the prothorax membracids give evidence of more recent structural developments. The most clear-cut characters which enable the separation of the AETALIONIDAE from the rest of the Jassoidea are those furnished by the venation of the tegmen. These characters are not secondary superficial ones selected for convenience, but persistent ones retained since the aetalionids first diverged from the main jassoid stem.

The ridged bosses on the first abdominal segment suggest comparison with the tymbals of cicadas. The primitive Australian cicada, *Tettigarcta*, has functionless tymbals in an identical position (Evans, 1941). Whether these structures are sound-producing organs, and whether functional or not, cannot be determined from the dried specimens which have been available for study. The cradling of the aedeagus in the fused parameres is another character which the AETALIONIDAE share with *Tettigarcta*. It is not intended to suggest by these comparisons that any particularly close degree of relationship exists between the two groups, but the characteristics shared in common are more probably due to the retention of ancient structural developments than the result of recent convergence.

The function of the apical tubular process of *Darthula* is unknown, although Haupt (1929) suggested it might act, in case of need, for a breathing tube for the last pair of spiracles. Carpenter (1939) has suggested that the Palaeorhyncha of the Lower Permian were aquatic, because the Archescytinid *Per-*

moscytina kansasensis Tillyard had a long terminal abdominal process. While this suggestion is not supported, the occurrence of a similar structure in *Darthula* may be a further example of the retention of an ancestral character.

In habits and structure the AETALIONIDAE are undoubtedly the most primitive surviving Jassoidea, and it is to be regretted that so little is known of their biology and that the species comprised in the genus *Aetalion* have never been critically studied.

Taxonomic Notes.

The genus *Aetalion* was defined by Latreille in 1809 and the type *Lystra reticulata* F., 1803, which is a synonym of *Cicada reticulata* L., 1758, was fixed by Latreille in 1810. The name was first amended, unnecessarily, to *Aethalion* in 1825 by Le Peletier and Serville.

Goding (1927) gives a list of the several described species belonging to the genus *Aethalion*. The list comprises fourteen species with several synonyms and also a few named varieties. In the same paper he lists the genera which, in his opinion, should be included in the AETHALIONINAE. All these genera, which are fourteen in number, apart from *Aethalion*, are membracid genera, although one genus, *Nicomia* Stål, while a true membracid, is possibly closer to *Aetalion* than are any of the others. In 1931 the same author divided the AETHALIONINAE into two tribes, the Aethalionini and the Tolanini. In the first-named he placed *Aethalion*, *Darthula* and *Coloborrhis* Germar, and in the latter *Porcorhinus* Goding and *Hemcicentrus* Melichar. *Coloborrhis* is a jassid belonging to the sub-family ULOPINAE, *Porcorhinus* a jassid belonging to the LEDRINAE and *Hemcicentrus* is a membracid.

Ulopa Fall. and related genera have been associated with *Aetalion* by several authors (e.g. Haupt, 1929) and species in the two groups resemble each other to the extent that both have retained certain primitive features in the structure of their heads. Nevertheless the ULOPINAE are true jassids and as such will be discussed in a later part of this series.

Signoret (1850) associated *Aethalion* with *Eurymela* Le P. and Serv. in his group "les Eurymelides," but *Eurymela*, which is an Australian genus, is widely separated from *Aetalion*. Metcalf in his recent Bibliography (1942) places *Endoiastus* Fowler in the AETHALIONIDAE, but it is really a membracid genus.

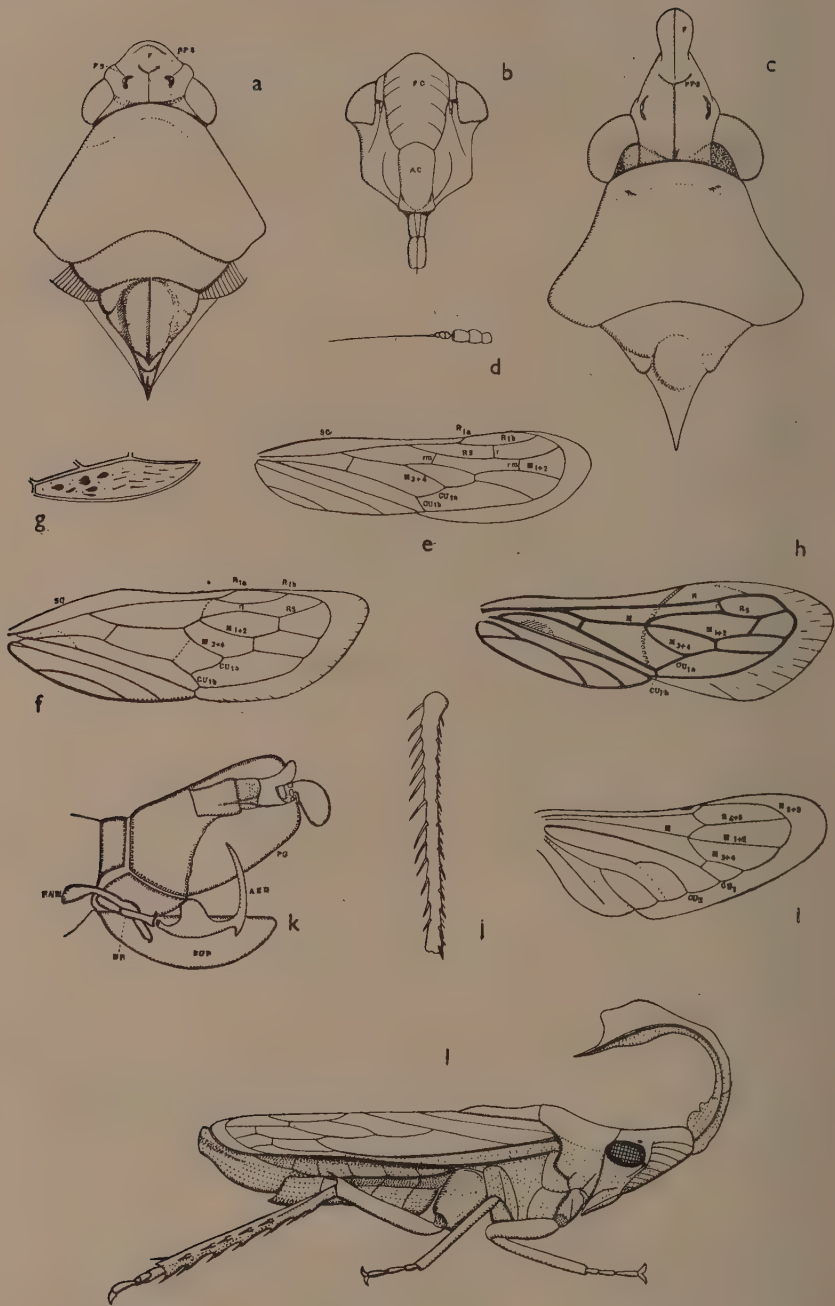
In 1832 Gray described the genus *Urophora* with the type *Urophora hardwickii* Gray. As this genus was preoccupied, Kirkaldy re-named it *Darthula* in 1900. At the same time he incorrectly attributed *Urophora* and its type to Westwood.

HYLICIDAE.

The family HYLICIDAE at present comprises fourteen genera. In spite of their abundance of distinctive characters these genera have formerly been placed close to *Penthimia* Germar and *Gypona* Germar, which they resemble in only a few essentially superficial characters.

Distribution.

Two genera have species which occur in tropical Africa and range from Uganda in the east to the Gold Coast in the west. The remainder have an Oriental distribution, their representatives occurring in Southern India, Assam, Burma, Java, Sumatra, Borneo, China and Formosa.



Size, Coloration and General Appearance.

In size the HYLICIDAE range from 10 to 17 mm. and in colour are predominantly black or brown. Their most striking characteristics are a large pronotum and scutellum, a flattened abdomen and the occurrence of a sparse covering of scales and hairs.

Food-plants and Habits.

These are apparently unknown.

Description.

The whole body is sparsely covered with hairs and scales.

Head. The head is longer than wide, the labium is short and the maxillary plates are wide. The ante-clypeus is large and is separated from the fronto-clypeus by a well-marked suture. The fronto-clypeus is wide and the prominent antennal ledges are short. The antennae are short and the basal segment is sometimes enlarged. The frontal sutures extend as far as the posterior margin of the face and may be continued on to the crown. The crown is well developed and consists partly of the frons, and in those species which have produced heads the prolongation is entirely of frontal origin. The ocelli, which are on the crown, are raised on prominences, and lie close to the posterior apices of the frontal sutures but posterior to the anterior apices of the postfrontal sutures. The separation of the frontal from the postfrontal sutures is a secondary development, the result of the anteriorly directed extension of the head. The hind margin of the crown is depressed.

Thorax. The pronotum is large and considerably wider posteriorly than anteriorly. The pro-episterna are usually partially, and sometimes entirely, concealed by the head. The scutellum, which is large, is raised medially and constricted laterally.

Legs. The fore tibiae, which are armed with short spines, are sometimes wide and flattened. The hind coxae are large and flattened and extend to the lateral margins of the thorax, and the hind tibiae have an armature of strong spines which are sometimes mounted on prominent bases.

Tegmina. The tegmina are long and narrow and have a wide corrugated appendix which extends around the apex as far as the costal margin. The costal margin, with which Sc is incorporated proximally, is usually curved inwards medially and the anal area is rounded and not angulate. Together with the rest of the body, the tegmina bear hairs and scales.

In those representatives having the most complete venation (e.g. *Kalasha nativa* Distant, fig. 2, e) the identity of the radial sector is readily ascertained. In others, in which a nodal line occurs, R_5 appears to arise from the media (fig. 2, f and h). The media has two branches, of which the anterior extends as far as the apex of the tegmen and the posterior is fused apically with Cu_{1a} . The nodal line is discussed in a later section.

Wings. The venation of the wing calls for no special comment since it is of the same basic type as that occurring in the JASSIDAE. In fig. 2, i, both branches of R have been

FIG. 2.—a. *Balala fulviventris*, head and thorax, dorsal aspect; b. *B. fulviventris*, head; c. *Traiguema nasuta*, head and thorax, dorsal aspect; d. *T. nasuta*, antenna; e. *Kalasha nativa*, tegmen; f. *B. fulviventris*, tegmen; g. *B. fulviventris*, cell of tegmen to show scales and hairs; h. *Hylica paradoxa*, tegmen; i. *H. paradoxa*, wing; j. *B. fulviventris*, hind tibia; k. *T. nasuta*, male genitalia; l. *Wolfella caternaulti*, lateral aspect.

Abbreviations.

AC., anteclypeus; AED., aedeagus; BP., basal plate; F., frons; FC., fronto-clypeus; FS., frontal suture; PAR., paramere; PFS., postfrontal suture; PG., pygophore; SGP., subgenital plate.

indicated as belonging to the radial sector, but as previously pointed out (Evans, 1946) they may represent R_1 and R_2 respectively.

Abdomen. The abdomen is wide and considerably flattened dorsally.

Male Genitalia. The male genitalia of only one species (*Traiguma nasuta* Distant) have been available for study and are illustrated in fig. 2, k. The sternite of the ninth segment is reduced and the pygophore is large and divided into two distinct sclerites. An elongated basal plate links the parameres with the base of the aedeagus and the latter is not in contact with the anal segment.

Discussion.

The venation and shape of the tegmina, the occurrence of a nodal line, the great development of the pronotum and scutellum and the possession of scales are sufficient characters to show that the HYLICIDAE are a well-defined and distinct natural family of early derivation from the common jassoid stem. The head, however, retains no traces of primitive features and the loss of the separate identity of the frons, the extension of the frons on to the crown, the loss of the maxillary sutures, the development of a transverse clypeal suture and the dorsal position of the ocelli are developments which have also occurred in several jassid groups, to which the HYLICIDAE are in no way closely related.

One character merits special mention: this is the occurrence of a nodal line in the tegmen. The nodal line, which is not of universal occurrence in the HYLICIDAE, consists of a thickened ridge which extends from the costal border at R_{1a} to the anal border at Cu_{1b} . Originally a line of weakness, such a transverse division of the tegmen into two parts occurred in several Palaeozoic Homoptera, especially in the tegmina of insects belonging to the family PROSBOLIDAE (e.g. *Prosbolia elongata* Martynov, 1928 and *Austroprosbolia maculata* Evans, 1943).

With recent Homoptera the nodal line is retained in its most complete form in cicadas belonging to the genus *Tettigarcta* White, but it occurs also, to a less extent, in nearly all other cicadas. Apart from the HYLICIDAE, no trace of such a line is retained in the tegmina of any Jassoids. Liu (1939), in describing a Hylicid (*Balala membracioidea*) from China, mentions the differentiation of the tegmen of this species into a membranous region and a coriaceous one. In commenting on Liu's paper, China (1941) states that such a differentiation of the tegmen does not indicate any relationship with the Heteroptera. This view is doubtless correct; nevertheless it is probable that the Heteroptera were derived from a Homopterous form which possessed a well-developed nodal line in the fore-wing. As the presence of a nodal line may confuse the issue with regard to the homologies of the various veins as demonstrated in fig. 2, e, f, and h, it is quite possible that the current interpretation of the venation of the fore-wings of the Heteroptera is incorrect.

List of Genera in the HYLICIDAE.

Ahenobarbus Distant (synonym of *Nacolus* Jacobi).

1918, *Faun. Brit. Ind. Rhyn.* 7 : 28.

Type—*Ahenobarbus assamensis* Distant (Assam).

Assiringia Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 255.

Type—*Assiringia exhibitata* Distant (Burma).

Balala Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 250.

Type—*Penthimia fulviventris* Walker (Assam, Burma, Borneo).

- Hatigoria* Distant.
1907, *Faun. Brit. Ind. Rhyn.* 4 : 258.
Type—*Hatigoria praeceus* Distant (Burma).
- Hemisudra* Schmidt.
1911, *Stettin. ent. Ztg* 72 : 228.
Type—*Hemisudra borneensis* Schmidt (Borneo).
- Hylica* Stål.
1863, *Trans. ent. Soc. Lond.* 1863 : 593.
Type—*Hylica paradoxa* Stål (Borneo).
- Kalasha* Distant.
1907, *Faun. Brit. Ind. Rhyn.* 4 : 254.
Type—*Kalasha nativa* Distant (Assam).
- Karasekia* Melichar.
1914, *Ergeb. 2te deuts. Zentr. Afr. Exped.* 1910, 1. (Zool., V. Homopt.) : 117.
Type—*Karasekia lata* Melichar (East Africa).
- Melliala* Hedicke.
1923, *Deutsch. ent. Z.* 1923 : 72 (new name for *Mellia* Schmidt, 1919, *Arch. Naturg.* 85 (A) 7 : 127).
Type—*Mellia granulata* Schmidt (China).
- Nacolus* Jacobi.
1914, *Sitzber. Ges. naturf. Fr. Berlin* 1914 : 318.
Type—*Nacolus gravioralis* Jacobi (Formosa).
- Parasudra* Schmidt.
1909, *Stettin. ent. Ztg* 70 : 263.
Type—*Parasudra borneensis* Schmidt (North Borneo).
- Sudra* Distant.
1907, *Faun. Brit. Ind. Rhyn.* 4 : 257.
Type—*Sudra notanda* Distant (Burma).
- Traiguma* Distant.
1907, *Faun. Brit. Ind. Rhyn.* 4 : 261.
Type—*Traiguma nasuta* Distant (Southern India).
- Wania* Liu (synonym of *Balala* Distant).
1939, *China J.* 31 : 267.
Type—*Wania membracoides* Liu (China).
- Wolfella* Spinola.
1852, *Mem. Mat. Fis. Soc. Ital. Sci. Modena* (Tavola Sinottica) 25 (1) : 97 ; 160.
Type—*Wolfella caternaultii* Spinola ("Guinea"; occurs in Uganda and West Africa).

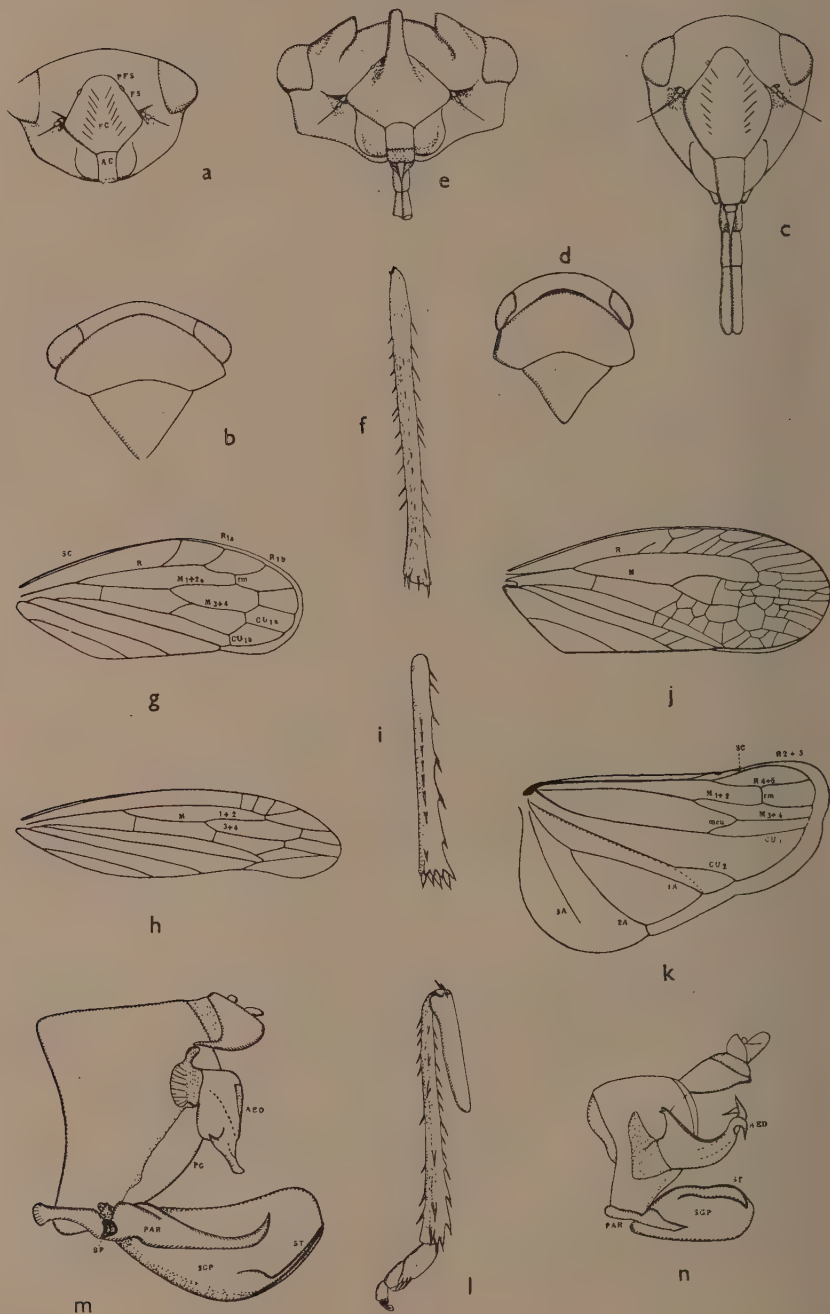
Taxonomic Notes.

Distant (1907) divided the GYPONINAE into two divisions, the Penthimiarina and the Hylcarina. In the latter division he placed *Hylica*, *Kalasha*, *Assiringia*, *Sudra*, *Hatigoria* and *Traiguma* and also four genera which rightly belong elsewhere, and he placed *Balala* in the Penthimiarina.

Schmidt (1909), while transferring *Balala* to its correct position in the Hylcini, followed Distant in believing this tribe to be included in the GYPONINAE, and Jacobi (1914) placed the Hylcini in the JASSINAE.

Further research may show that the genera of the HYLICIDAE can be grouped into sub-families, but at present I have failed to find adequate characters on which to base any natural divisions.

The reasons for the removal of the HYLICIDAE from any close degree of association with *Gypona* and *Penthimia* will be made clear in that part of this series which deals with these genera.



EURYMELIDAE (fig. 3).

The EURYMELIDAE comprise twenty-three genera. Until raised to the status of a family (Evans, 1934) they were regarded as belonging to the BYTHOSCOPIIDAE (e.g. China, 1926).

Distribution.

The family is confined to Australia and the neighbouring islands of Tasmania, New Caledonia and New Guinea.

Size, Coloration and General Appearance.

In size the EURYMELIDAE range from 4 to 14 mm. There are three sub-families, the EURYMELINAE, the IPOINAE and the POGONOSCOPIINAE. The EURYMELINAE comprise wedge-shaped insects with tectiform tegmina, which are usually predominantly black and have vivid markings of white, red, yellow or blue. The IPOINAE are brown or grey, or white and black in coloration; their tegmina frequently have a mottled appearance and sometimes they are hyaline. The POGONOSCOPIINAE are brown in colour and some species have pale markings on their tegmina. Several species in both the EURYMELINAE and the IPOINAE have a very variable colour pattern.

Food-plants.

The EURYMELINAE feed exclusively on the branches of eucalypts and the POGONOSCOPIINAE on their roots. Several of the IPOINAE also feed on eucalypts, but others feed on *Loranthus* growing on eucalypts and on *Casuarina* and *Eremocitrus*.

Habits.

Adults and nymphs are gregarious and are attended by ants (Evans, 1931); the POGONOSCOPIINAE actually live inside ants-nests. Eggs are laid in groups, in slits made by the females in the branches of the food-plant, and the "nests" are concealed beneath a frothy secretion which hardens on exposure to air. The nymphs, which have their-legs widely spread, do not jump if disturbed.

Description.

Head. With a few exceptions, the face of the head is somewhat flattened and wider than long. In the EURYMELINAE and IPOINAE the labium is short and only two segments are visible. The labium of the POGONOSCOPIINAE is long and the proximal segment is exposed. The transverse suture of the clypeus is strongly developed, the maxillary plates are wide and the fronto-clypeus is diamond-shaped. The antennal ledges arise from the fronto-clypeus slightly posterior to their lateral angles and the antennae are short. The frontal

FIG. 3.—a. *Eurymeloides pulchra*, head; b. *E. pulchra*, head and thorax, dorsal aspect; c. *Pogonoscopus myrmex*, head; d. *P. myrmex*, head and thorax, dorsal aspect; e. *Cornutipoides tricornis*, head; f. *P. myrmex*, hind tibia; g. *Ipo pellucida*, tegmen; h. *Bakeriola procurrens*, tegmen; i. *I. pellucida*, hind tibia; j. *Eurymelops generosa*, tegmen; k. *E. pulchra*, wing; l. *E. bicincta*, hind tibia and tarsus; m. *E. bicincta*, male genitalia; n. *Eurymelita terminalis*, male genitalia.

Abbreviations.

AC., anteclypeus; AED., aedeagus; FC., fronto-clypeus; FS., frontal suture; PAR., paramere; PFS., postfrontal suture; PG., pygophore; SGP., subgenital plate; St., style.

and postfrontal sutures form a straight line or an even curve and the ocelli, which are always ventral in position, lie against them at the point where the postfrontal meet the frontal sutures. No trace remains of a frons as a distinct sclerite. The crown is narrow and a coronal suture, if retained at all, is ill defined.

Thorax. The thorax calls for no special comment, except to note that the pro-episterna are partially concealed by the head.

Legs. The tibiae of all three pairs of legs are quadrilateral in section although the hind tibiae of the POGONOSCOPINAE, which are very long, have a somewhat rounded appearance. The hind tibiae of the EURYMELINAE and the IPOINAE bear one or a few spines mounted on prominent bases, in addition to two other rows of small unmounted spines.

Tegmina. The tegmina may be hyaline, or opaque and coriaceous, and have a simple or a reticulate venation. The appendix may be small or extensive. In those forms having a reticulate venation the homologies of the various veins are difficult to determine. In others, where the radius has two branches, these are clearly R_{1a} and R_{1b} and the radial sector is not developed. Many species have additional veinlets which extend from the radius to the costal border. Both branches of the media (M_{1+2} and M_{3+4}) extend to the apex of the tegmen and in a few species M_3 and M_4 are present as separate veins. Cu_1 has the usual two branches, which are common to all the Jassoidea, apart from the AETALIONIDAE.

Wings. The venation of the wings usually follows the same plan as in the JASSIDAE, but individual variations occur in which subsidiary cross-veins are developed and M_{1+2} may be present as M_1 and M_2 .

Male Genitalia. The male genitalia retain no trace of a separate sternite of the ninth segment and there is but little pygophore development. The apodeme of the aedeagus is in contact with the ventral posterior angle of the anal (tenth) segment, and the orifice is ventral in position. The basal plate, which separates the parameres, is small and not in contact with the aedeagus. The sub-genital plates are wide and flap-like in both the EURYMELINAE and the POGONOSCOPINAE. In the IPOINAE they may be either wide or narrow. Accessory styles may be present as processes arising either from the dorsal or the ventral margin of the sub-genital plates.

Discussion.

The venation of the tegmina of the EURYMELIDAE suggests that they are a derivation from the Jassoid stem separate from that which gave rise to the JASSIDAE. The radial sector is absent in the EURYMELIDAE but present in the JASSIDAE, and the anterior branch of the media, which extends as far as the apex of the tegmen in the EURYMELIDAE, is reduced to a cross-vein in the JASSIDAE, being distally fused with the radial sector. The other outstanding diagnostic character is found in the structure of the male genitalia, where the aedeagus has lost contact with the basal plate and has developed wide basal apodemes which lie beneath the segmental membrane. This is presumably a secondary development, and the condition found in the AETALIONIDAE where the aedeagus is in contact with the basal plate and also with the base of the anal segment the more primitive one.

The structure of the head is remarkably uniform throughout the group and although one species (*Cornutipoides tricornis* Evans, fig. 3, e) has developed horns on the fronto-clypeus and the vertex, and others have the fronto-clypeus anteriorly produced or spatulate, these are secondary developments of no structural significance. The head is primitive in character to the extent that the frontal and postfrontal sutures are entirely on the face and lie well away from the hind margin of the head, likewise in the position of the ocelli, but otherwise it has retained no trace of its ancestral pattern.

The IPOINAE are the most generalised group and the POGONOSCOPIINAE are derived from the EURYMELINAE. The present distribution of the EURYMELIDAE, and the fact that, with one exception, the POGONOSCOPIINAE are confined to Western Australia, suggests that the family may have arisen in Western Australia in cretaceous times, when that part of the present Australian continent was separated from Eastern Australia by a wide sea. In being ant-attended the EURYMELIDAE resemble the AETALIONIDAE and the MEMBRACIDAE. The association of ants with representatives of all three families is doubtless linked with the fact that all have sedentary and gregarious habits and also possibly with their physiology of digestion and the structure of their filter chambers. The reduced eyes and the long legs of the POGONOSCOPIINAE are characters found in many myrmecophiles, and arthropods generally, which live in the dark.

List of Genera comprised in the EURYMELIDAE.

EURYMELINAE.

Eurymela Le Peletier and Serville.

1828, *Encyc. Méth.* 10 : 603.

Type—*Eurymela fenestrata* Le Peletier and Serville (Australia).

Eurymelias Kirkaldy (synonym of *Eurymeloides* Kirkaldy).

1907, *Bull. Hawaii. Sug. Ass. Exp. Sta.* 3 : 29.

Type—*Eurymelias hyacinthus* Kirkaldy (Australia).

Eurymellella Evans.

1939, *Trans. Roy. Soc. S. Aust.* 63 : 47.

Type—*Eurymellella tonnoiri* Evans (Australia).

Eurymellessa Evans.

1933, *Trans. Roy. Soc. S. Aust.* 57 : 88.

Type—*Eurymeloides moruyana* Distant (Australia).

Eurymelita Evans.

1933, *Trans. Roy. Soc. S. Aust.* 57 : 89.

Type—*Eurymela terminalis* Walker (Australia).

Eurymeloides Kirkaldy.

1906, *Bull. Hawaii. Sug. Ass. Exp. Sta.* 1 (9) : 354.

Type—*Eurymeloides bicincta* Erichson (Australia).

Eurymelops Kirkaldy.

1906, *Bull. Hawaii. Sug. Ass. Exp. Sta.* 1 (9) : 350.

Type—*Eurymela rubrovittata* Amyot and Serville (Australia).

Pauroeurymela Evans.

1933, *Trans. Roy. Soc. S. Aust.* 57 : 79.

Type—*Eurymela ampicincta* Walker (Australia).

Platyeurymela Evans.

1933, *Trans. Roy. Soc. S. Aust.* 57 : 78.

Type—*Eurymela semifascia* Walker (Australia).

POGONOSCOPIINAE.

Australoscopus China.

1926, *Trans. ent. Soc. Lond.* 1926 : 296.

Type—*Australoscopus whitei* China (Central Australia).

Lasioscopus China.

1926, *Trans. ent. Soc. Lond.* 1926 : 294.

Type—*Eurymeloides acmaeops* Jacobi (Western Australia).

Pogonoscopus China.

1924, *Ann. Mag. nat. Hist.* (9) 14 : 259.

Type—*Pogonoscopus myrmex* China (Western Australia).

IPOINAE.

Anacornutipo Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 163.Type—*Eurymela lignosa* Walker (Australia).*Anipo* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 159.Type—*Eurymela porriginosa* Signoret (Australia).*Bakeriola* Evans (new name for *Ipocerus* Evans).1939, *Pap. Roy. Soc. Tasm.* 1938 : 17.1934, *Trans. Roy. Soc. S. Aust.* 58 : 165.Type—*Ipo procurrens* Jacobi (W. Australia).*Citripo* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 161.Type—*Citripo flandersi* Evans (Australia).*Cornutipo* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 164.Type—*Cornutipo scalpellum* Evans (Australia).*Cornutipoides* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 164.Type—*Cornutipoides tricornis* Evans.*Ipo* Kirkaldy.1906, *Bull. Hawaii, Sug. Ass. Exp. Sta.* 1 (9) : 464.Type—*Ipo ambita* Kirkaldy (a synonym of *Cicada pellucida* Fabricius) (Australia).*Ipoella* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 157.Type—*Ipoella fidelis* Evans (Australia).*Ipoides* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 155.Type—*Ipoides hackeri* Evans (Australia).*Katipo* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 160.Type—*Eurymeloides rubrivenosus* Kirkaldy (Australia).*Opio* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 165.Type—*Bythoscopus multistrigia* Walker (Australia).*Pauripo* Evans.1934, *Trans. Roy. Soc. S. Aust.* 58 : 161.Type—*Pauripo insularis* Evans.*Taxonomic Notes.*

It has already been mentioned that until 1934 the EURYMELIDAE were regarded as belonging to the BYTHOSCOPIINAE, a subfamily which served for the reception for all leaf-hoppers having ventral ocelli, although Kirkaldy (1907) used the term Eurymelini instead of BYTHOSCOPIINAE for an identical artificial grouping.

Baker (1915) was the first to question the placing of *Eurymela* in the BYTHOSCOPIIDAE and suggested that as the EURYMELIDAE had strong membracid affinities they should be examined with a view to seeking relationships with the Aetalionids.

Oman (1936) is of the opinion that *Idiocerus* Lewis and related genera belong to the EURYMELIDAE but gives no reasons to support his suggestion. The wide separation of *Eurymela* from *Aetalion* is abundantly clear from the descriptions

and illustrations given in the foregoing pages, and the lack of any close degree of relationship between *Eurymela* and *Idiocerus* and *Bythoscopus* Germar will be made evident in parts of this series which are to follow.

REFERENCES.

- ASHMEAD, W. H., 1889, A Generic synopsis of the BYTHOSCOPIIDAE. *Ent. amer.* 5 : 125.
- BAKER, C. F., 1915, Studies in Philippine Jassoidea, Pt. 2. *Philipp. J. Sci.* 10 (D) : 49.
- CARPENTER, F. M., 1939, The Lower Permian Insects of Kansas, Pt. 8. *Proc. Amer. Acad. Arts Sci.* 73 (3) : 29.
- CHINA, W. E., 1926, A new genus of BYTHOSCOPIINAE from Western Australia. *Trans. ent. Soc. Lond.* 1926 : 289.
- , 1941, A synonymic note on *Wania membracioidea* Liu. *Ann. Mag. nat. Hist.* (11) 7 : 255.
- COLTHURST, I., 1931, The Biology of *Darthula hardwicki*. *J. Darjeeling nat. Hist. Soc.* 6 : 70.
- EVANS, J. W., 1931, Notes on the Biology and Morphology of the EURYMELINAE. *Proc. Linn. Soc. N.S.W.* 56 : 210.
- , 1934, A Revision of the IPOINAE. *Trans. Roy. Soc. S. Aust.* 58 : 149.
- , 1939, A contribution to the study of the Jassoidea. *Pap. Roy. Soc. Tasm.* 1938 : 19.
- , 1941, The Morphology of *Tettigarcta tomentosa* White. *Pap. Roy. Soc. Tasm.* 1940 : 35.
- , 1943, Upper Permian Homoptera from N.S.W. *Rec. Aust. Mus.* 21 : 180.
- , 1946, A Natural Classification of Leaf-hoppers, Pt. 1. *Trans. R. ent. Soc. Lond.* 96 : 47-60.
- FOWLER, W. W., 1897, *Biologia Centrali Americana* 2 : 169.
- GODING, F. W., 1925, Synopsis of the MEMBRACIDAE of Chile. *Rev. chil. Hist. nat.* 27 : 118.
- , 1927, Revision of the MEMBRACIDAE of South America and the Antilles. *J. N.Y. ent. Soc.* 35 : 183.
- , 1931, Classification of the Old World MEMBRACIDAE. *J. N.Y. ent. Soc.* 39 : 299.
- GRAY, G. R., 1832, in Griffiths, *Cuvier's Anim. Kingdom, Ins.* 2 : 261.
- HAUPT, H., 1929, Neueinteilung der Homoptera-Cicadina nach phylogenetisch zuwertenden Merkmalen. *Zool. Jahrb. (Syst.)* 58 : 173.
- JACOBI, A., 1914, Bemerkungen über JASSINAE. *SB. Ges. naturf. Fr. Berlin* 1914 : 318.
- KIRKALDY, G. W., 1900, Bibliographical and nomenclatorial notes on the Rhynchota No. 1. *Entomologist* 33 : 242.
- , 1907, Leaf-hoppers, Supplement. *Bull. Hawaii Ass. Exp. Sta.* 3.
- LATREILLE, P. A., 1809, in Humboldt & Bonpland, *Voy. Reg. Equin. Nouv. Continent* (2) 2 : 378.
- , 1810, *Considérations générales Crustacés Arachnides Insectes* : 263, 434.
- LE PELETIER DE ST. FARGEAU, A. M. L., and SERVILE, J. G., 1825, in Olivier, *Encyc. méthodique* 10 (2) (Ins.) : 765.
- LIU, G. K. C., 1939, On a new genus of Homoptera from Anhwei. *China J.* 31 (6) : 295.
- MARQUES, L. A. de R., 1928, Biologia do membracioidea *Aetalion reticulatum*. *Bol. Inst. biol. Def. agric. Rio de J.* 6 : 1.
- MARTYNOV, A., 1928, Permian fossil insects of North-East Europe. *Trav. Mus. géol. Acad. Sci. U.R.S.S.* 4 : 1.

METCALF, Z. P., 1942, A Bibliography of the Homoptera, 2.

OMAN, P. W., 1936, A generic revision of American BYTHOSCOPIINAE and South American JASSINAE. *Kansas Univ. Sci. Bull.* 24 : 348.

SCHMIDT, E., 1909, Zwei neue Jassiden aus dem Stettiner Museum. *Stettin. ent. Ztg* 70 : 263.

SIGNORET, A. V., 1850, Sur le Groupe des Eurymelides. *Ann. Soc. ent. Fr.* (2) 8 : 497.

STÅL, C., 1869, Bidrag till membracidernas kannedom. *Öfvers. Vetensk. Akad. Förh. Stockh.* 1869 : 231.

Vol. 97. Part 3. Pp. 55-73, 10 figs.

22nd July, 1946.

IMP. INST. ENT.
LIBRARY

13 AUG 1946

SERIAL
DATE

Eu. 344

THE

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

- X HALL, W. J., D.Sc., F.R.E.S. New or little known
species of DIASPIDIDAE (Coccoidea) from Africa

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 5s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.	} <i>Vice-Presidents</i> .
C. B. WILLIAMS, M.A., D.Sc.	
H. B. WILLIAMS, LL.D.	

A. WELT, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,
D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Registrar :

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RATT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

I. HOBBY, M.A., D.Phil.

PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

A. F. BAUFOR-BROWNE, F.R.S.E.

S. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. DENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. **British National Committee for Biology** (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. **Local Committee of Management of Wicken Fen.**

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. **National Trust for Places of Historic Interest or Natural Beauty.**

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. **New Forest Association.**

Mr. W. Fassnidge, appointed 1934.

5. **New Forest Joint Committee.**

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. **Royal Meteorological Society. Phenological Committee.**

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. **Biology War Committee.**

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. **Council for the Promotion of Field Studies.**

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. **Joint Bioclimatic Committee.**

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

NEW OR LITTLE KNOWN SPECIES OF DIASPIDIDAE ¹ (COCCOIDEA) FROM AFRICA

By W. J. HALL, D.Sc., F.R.E.S.

(Imperial Institute of Entomology.)

Manuscript received 1st October, 1945.

(Read 16th January, 1946.)

WITH 10 TEXT-FIGURES.

Aonidiella atomaria sp. n. (fig. 1).

Scale of adult female circular, low convex, white but, although thin, sufficiently opaque to mask the outline of the body; thinner at the extreme margin and semitranslucent; exuviae central, very dark brown in fully developed scales but paler in early stages; ventral scale very thin and transparent, remaining adherent to the host plant.

Male scale smaller than that of the female, oval and opaque white with pale yellow exuvia.

Diameter of scale of adult female, 1.50-1.75 mm.

Prosomatic region strongly sclerotised in mature examples and of the reniform shape typical of the genus. Ventral dermis closely stippled except in the median area posterior to the mouthparts where the stippling gives way to fine imbrications. Margin with a small inconspicuous flatly rounded thoracic tubercle. Pygidium with three pairs of lobes, the median pair being larger and more heavily sclerotised than the lateral lobes; the median lobes are notched near the apex both on the inner and outer margins, the lateral lobes are notched only on the outer margin. Seven well-developed plates anterior to the third lobe. Dorsal ducts in four rows of which the innermost, arising from between the median and second lobes, is ill defined and consists of 4 to 6 pores. Marginal paraphyses extremely minute. Perivulvar pores in four groups, anterior laterals 3-10, posterior laterals 2-10 (average of 27 examples 7:6). Perivulvar apophyses and scleroses wanting although there are traces of the latter in some specimens. Fenestrations absent. Ducts present in submarginal clusters on the three prepygidial abdominal segments.

On undersurface of leaves of unidentified host plant. BELGIAN CONGO: Dilolo (*T. D. A. Cockerell*), 26.vii.31.

This species comes closest to *A. eugeniae* Hempel described from Brazil on *Eugenia* sp., from which it differs in having perivulvar pores and the lateral lobes lacking a pre-apical notch on the inner margin. According to McKenzie (1938, *Microentomology* 3:9) there is every reason to suppose that *eugeniae* was introduced into Brazil, probably from Africa.

Lindingaspis penniseti sp. n. (fig. 2).

Scale of adult female large, flat, subcircular, dull grey-brown in colour; exuviae very dark brown almost black, shiny but coated with a film of dull grey-brown secretory

¹ The species described in this paper were found amongst material sent to the Imperial Institute of Entomology for determination at various times. The types of the new species are in the British Museum (Natural History).

matter. Under surface a dark bluish-brown. Ventral scale very thin, remaining adherent to the host plant except for traces round the margin.

Male scale not seen.

Diameter of scale of adult female, 3-4 mm.

Body of fully developed female large, membranous and roughly circular in outline. Thoracic tubercles very indistinctly represented. Pygidium with a well-defined sclerotic

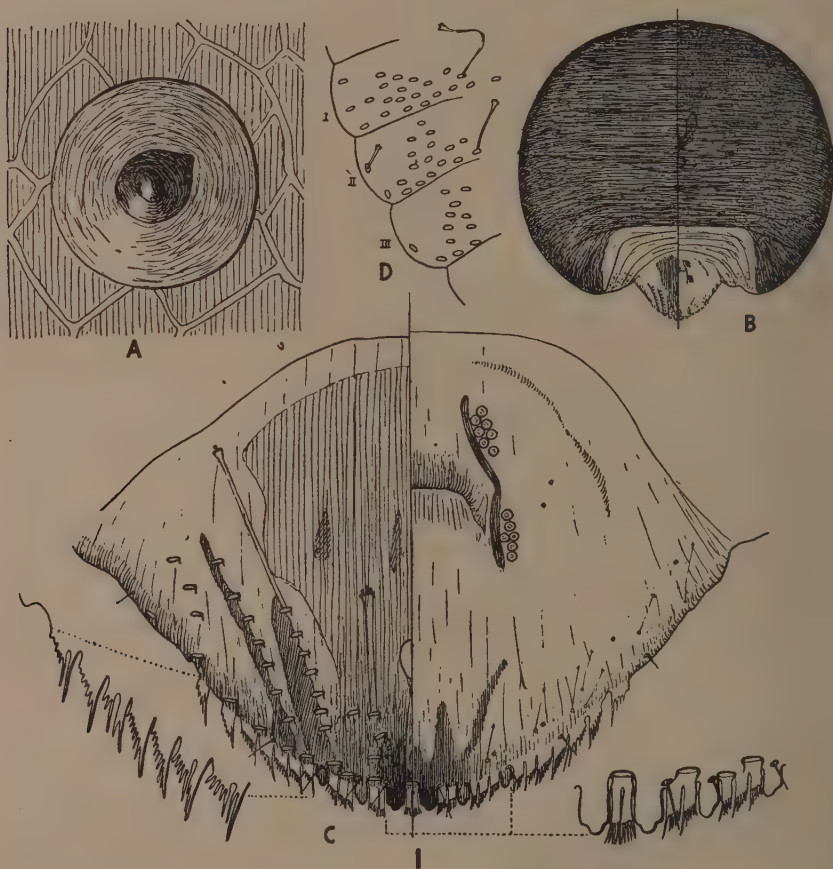


FIG. 1.—*Aonidiella atomaria* sp. n. : Adult female; A, Scale in situ on leaf; B, Body; C, Pygidium; D, Lateral margins of prepygidial segments.

pattern. Pygidial lobes in three pairs, the lobes all being of much the same size and shape, nearly as broad as long and with the outer edge falling away evenly and lacking any evidence of a lateral notch. Plates of the pygidial fringe as in *L. rossi* (Maskell) but paraphyses relatively shorter. Dorsal pores numerous, of relatively uniform size with the exception of 7-9 pores at the extreme margin, in the interlobular spaces, which are rather larger and have definitely larger capitate heads. Perivulvar pores in five groups, median, 0-9; anterior laterals, 12-32; posterior laterals, 7-24 (average of 17 examples, 3:21:17).

Microducts present marginally on all segments from the 6th segment to the metathorax. Anal orifice situated near the centre of the pygidium.

On *Pennisetum* sp. UGANDA: Kampala (*H. Hargreaves*), 6.iv.29.

This species comes close to *L. magnifica* Mckenzie, *L. rossi* (Maskell) and those forms described as varieties of them but differs in its larger size, more numerous

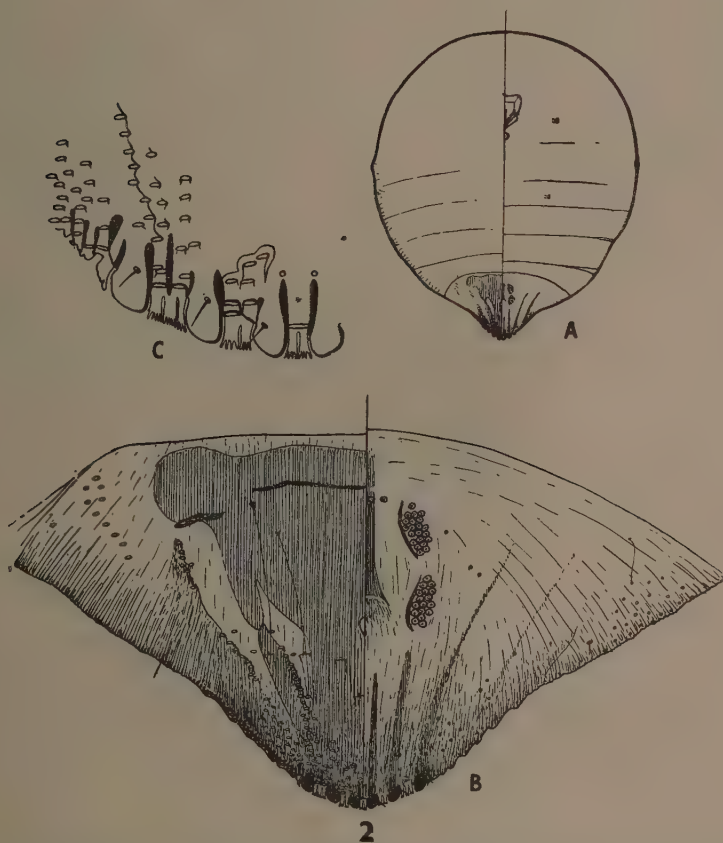


FIG. 2.—*Lindingspis penniseti* sp. n.: Adult female; A, Body; B, Pygidium; C, Portion of margin of pygidium further enlarged.

perivulvar pores, including the presence of a median group, and the absence of any trace of a lateral notch on the outer margins of the 2nd and 3rd pygidial lobes. Unlike *L. opimus* (Silvestri) it lacks the five large latero-marginal glands characteristic of that species. *L. penniseti* has only a single plate anterior to the third pair of lobes as in *rossi* Maskell, whereas in *rossi* var. *colae* Laing there are two, and in *rossi* var. *ferrandii* Malenotti there are three.

Marginaspis gen. n.

Belonging to the tribe Aspidiotini. Body with the margin strongly sclerotised, a prothoracic tubercle and a conspicuous thoracic indentation. Pygidium acute with four groups of perivulvar pores. Pygidial lobes in three pairs, the lobes being of elongate form and conspicuous. Interlobular plates truncate, fringed apically and of much the same length as the lobes. Three plates anterior to the third lobe followed by two strongly sclerotised spurs set close together. Margin beyond the spurs strongly sclerotised and serrated as far as the seta marking the fourth segment. Marginal paraphyses small but clearly developed, arising from the basal angle of each lobe with an intermediate one in the space separating the second and third lobes. Beyond the third lobe the paraphyses, progressively diminishing in size and closely set, continue as far as the seta marking the fourth segment. Anal orifice situated near the centre of the pygidium and relatively large.

Scale of the adult female, in the type species, flat and hemispherical in outline with the exuviae so close to the flattened margin as to appear marginal. Male scale similar in form but smaller.

The ventral dermis of both larval and nymphal exuviae incorporated in the ventral scale of the adult female and in the male scale the larval exuvia so incorporated.

Genotype :—*Marginaspis thevetiae* sp. n.

This genus appears to come between *Lindingaspis* MacGillivray and *Acutaspis* Ferris. It differs from both in having well-developed and conspicuous lobes and plates, in the presence of three well-developed plates anterior to the third pygidial lobe followed by a pair of conspicuous sclerotised spurs.

***Marginaspis thevetiae* sp. n. (fig. 3).**

Scale of adult female flat and roughly hemispherical in outline, lying on the under-surface of the leaf with the flattened portion of the margin resting against the very narrow thickened rim formed by the turning under of the extreme margin of the leaf. Colour chocolate, exuviae black or very dark brown and placed so close to the flattened edge as to appear marginal. Ventral scale thin but persistent round the margin to a greater or lesser degree.

Male scale similar to that of the female in shape but very much smaller, with only a very narrow fringe of the ventral scale persisting round the margin; exuvia black or very dark brown.

In the adult female scale the ventral portion of the nymphal exuvia, with that of the larval exuvia incorporated, is conspicuous, extending usually far beyond the part of the ventral scale persisting round the margin but let into it and partially covering the sublying adult female. In the male scale the ventral portion of the larval exuvia is relatively even more prominent as the marginal fringe of the ventral scale persisting is very narrow.

Length of scale of adult female, 3 mm.; breadth 1.50–1.75 mm.

Mature female with a strongly sclerotised marginal zone and a deep thoracic marginal indentation on either side. Prothoracic tubercle small and flatly rounded. On the dorsal aspect of the anterior margin, and lateral margin as far as the metathorax, a few unusually long setae occur at wide intervals. Pygidium acute, with a well-defined sclerotic pattern and with three pairs of rather long and narrow lobes; the median and second lobes have a distinct notch on the outer edge and the outer margin of the third lobe may have from one to several notches. The plates are much the same length as the lobes and finely fringed apically; there are two between the median lobes and between the median and second lobes and three between the second and third lobes, of which the innermost is extremely slender and inconspicuous. Beyond the third lobes there are three plates and anterior to these two strongly sclerotised spurs. Short club-shaped paraphyses occur in each interlobular space and beyond the third lobes a series of short closely set paraphyses extends as far as the seta

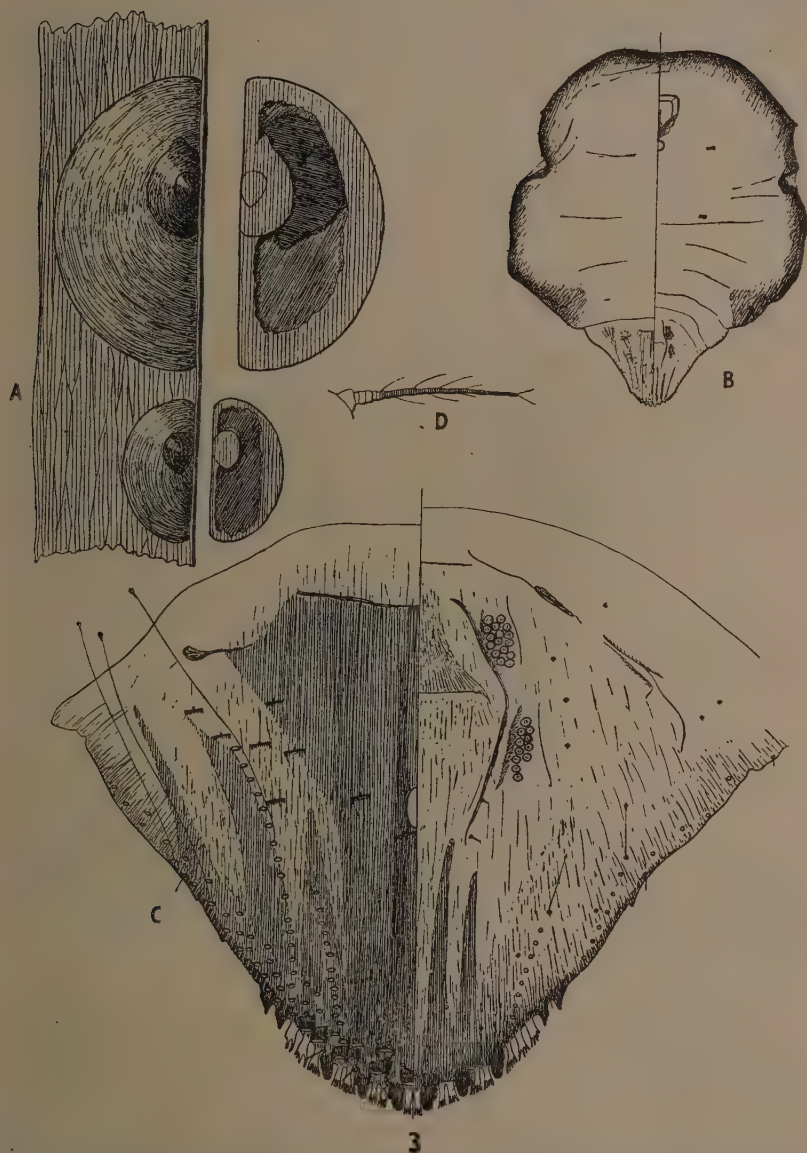


FIG. 3.—*Marginaspis thevetiae* sp. n.: A, Male and female scales in situ on leaf; on right same scales seen from ventral aspect; B, Body of adult female; C, Pygidium; D, Larval antenna.

on the fourth segment, the margin in this region is strongly sclerotised and serrated. Marginal pores, as far as midway between the third lobe and first marginal spur, large. Marginal pores anterior to this, and dorsal pores, small. Two well-defined series of dorsal pores run from the space between the second and third lobes and from between the first spur and third lobe. Anal orifice situated about the centre of the pygidium. Perivulvar pores in four groups, anterior laterals 13-20, posterior laterals 7-16 (average of 20 examples 16:11). Ventral dermis with a few microducts marginally and two series running inwards—one from just anterior of the third lobe, the other from anterior of the second spur. Scattered micropores with very short ducts occur all round the margin anterior to the 4th abdominal segment, and on the prepygidial segments there are, in addition, some micropores with relatively long ducts.

On *Thevetia neriifolia* (Apocynaceae). SIERRA LEONE: Njala (*E. Hargreaves*), 10.x.32. On the under surface of the leaves.

***Melanaspis gliricidia* sp. n. (fig. 4).**

Scale of the adult female circular, convex, very dark brown almost black with surface roughened by rather regular concentric laminations; texture thick but brittle and shiny black when viewed from the under surface. Exuviae black or very dark brown. Ventral scale very delicate and thin, remaining attached to the host plant. The scales are usually partially hidden beneath flakes of bark and as a greater or lesser amount of extraneous matter is also incorporated they are relatively inconspicuous.

Male scale similar to that of the female but much smaller, oval and with black exuvia.

Diameter of scale of adult female, 1.5 mm.

Body of adult female circular, dermis membranous. Pygidium short and somewhat obtuse, with a well-defined sclerotic pattern. Pygidial lobes in three pairs, all the lobes of much the same size, broader than long, small and inconspicuous; median pair set close together, rounded at the apex with a distinct notch on the outer lateral margin; second and third lobes similar but with two notches on the outer margin. Beyond the 3rd lobe there are five more or less evenly spaced marginal spurs. Plates small and inconspicuous, bifurcate at the apex; two occur between the median lobes and a pair in the other interlobular spaces, as well as a pair between the third lobe and first spur. Marginal paraphyses as illustrated in fig. 4, D. A conspicuous club-shaped paraphysis arises from the outer angle of the second and third lobes; from the outer angle of the median lobe a conspicuous paraphysis also arises but it is of different form, the terminal portion being detached; there are indications that there is a pore or seta situated at the broadened anterior apex of the basal portion and again in the circular detached portion, but the sclerotisation of the tissues obscures the nature of these structures. Other paraphyses smaller and extending as far as the anterior spur but becoming progressively shorter. Dorsal pores small with extremely long slender ducts in two definite series arising from between the second and third lobes and from the base of the first spur. Perivulvar pores in four very poorly developed groups; in only one individual were all four groups represented but in every individual at least one group was present, the maximum number in any one group was 4, the usual number was either one or two. Ventral dermis in a rather wide area round the posterior lateral group of perivulvar pores exhibits a faint but clearly discernible reticulate ornamentation. Ventral dermis also with a few micropores in the marginal area. Anal orifice towards the apex of the pygidium. Anterior to the pygidium there are a few scattered microducts and short setae all round the margin of the body, the microducts are nowhere more than a few but tend to be more numerous marginally on the abdominal segments, while the setae are more numerous in the frontal area. On the dorsal dermis of the first abdominal segment, situated submarginally on either side, is a distinct boss.

On *Gliricidia maculata* (Leguminosae), SIERRA LEONE: Njala (*E. Hargreaves*), 7.xii.32, No. 550, and on ? (*E. Hargreaves*), No. 548.

The specimen selected as "type" is an early adult female, as the older and much larger individuals were for the most part heavily parasitised.

This species is extremely close to *Aonidiella chrysobalani* Leonardi, which in my opinion is referable to the genus *Melanaspis*. It differs from Leonardi's

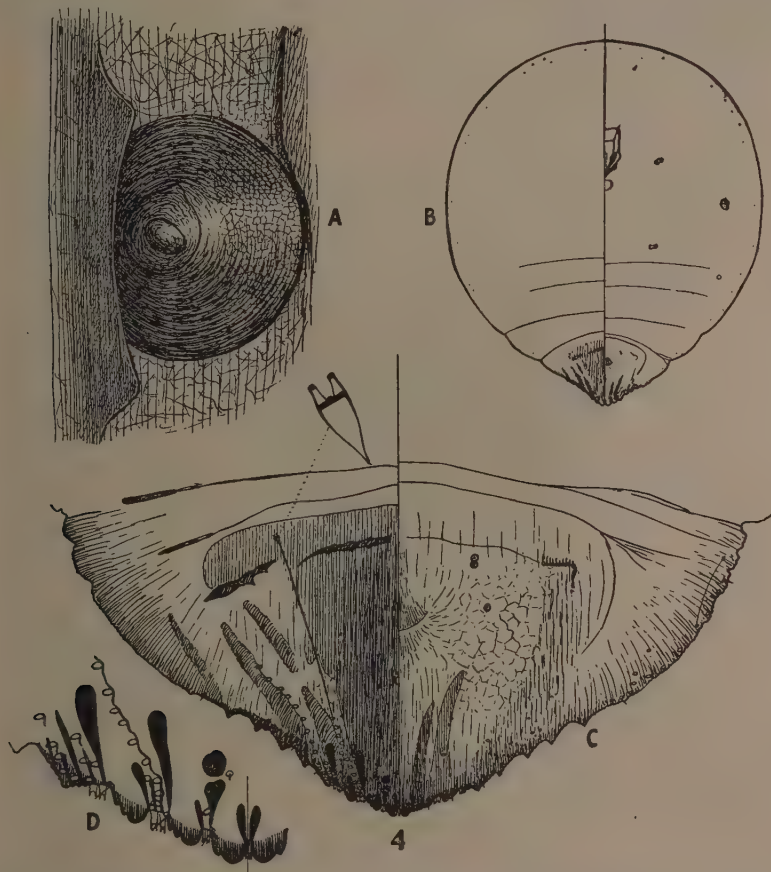


FIG. 4.—*Melanaspis gliricidia* sp. n. : Adult female; A, Scale in situ; B, Body; C, Pygidium; D, Portion of margin of pygidium further enlarged.

description and figures in the nature of the paraphysis associated with the outer angles of the median lobes, the paraphyses anterior of the first spur being more slender, the presence of perivulvar pores, the reticulated ornamentation of the ventral aspect of the pygidium, the presence of a boss submarginally on the first abdominal segment and the more prominent nature of the five spurs on the lateral margins of the pygidium.

If it were not for the different nature of the paraphysis associated with the

outer angle of the median lobe this species might well be considered a geographical form of *chrysobalani*, but the divided character of this paraphysis is so marked that it is thought advisable to describe it as a new species.

In addition to *chrysobalani* and *gliricidia* four other species known from the African continent are referable to the genus *Melanaspis*:—1. *Chrysomphalus* (*Pseudischchnaspis*) *corticosis* Brain. Common in S. Africa on a wide range of host plants and in S. Rhodesia on *Royena pallens*. 2. *Aonidiella inopinata* Leonardi from Egypt on apricot, pear and apple. 3. *Aonidiella monotes* Hall from S. Rhodesia on *Monotes glaber*. 4. *Chrysomphalus phenax* Cockerell from S. Africa on *Acacia horrida* and from S. Rhodesia on *A. karroo*.

These six species may be separated by the following key:—

1. Perivulvar pores present 2.
- Perivulvar pores absent 3.
- 2(1). Perivulvar pores in five well-developed groups; paraphyses arising from the outer angles of the median lobes truncheon-shaped; dorsal pores in the 2nd and 3rd interlobular spaces numerous and crowded, *corticosis* Brain.
- Perivulvar pores poorly developed, never more than four groups and with very few pores in each group; paraphyses arising from the outer angles of the median lobes with the terminal portion detached; dorsal pores in the 1st and 2nd interlobular spaces much less numerous and crowded *gliricidia* sp. n.
- 3(1). Paraphyses anterior to the 3rd lobes poorly developed and inconspicuous; dorsal pores in the 1st and 2nd interlobular spaces, if present, very few, minute and inconspicuous *monotes* Hall.
- At least two, often more, well-developed paraphyses anterior to the 3rd lobes; dorsal pores of the interlobular series clearly visible 4.
- 4(3). Paraphyses relatively short, stout and of more or less uniform length.
- Pores of the series arising from the 2nd interlobular space oval in shape *inopinata* Leonardi.
- Paraphyses not of uniform length. Pores of the series arising from the 2nd interlobular space circular and relatively smaller 5.
- 5(4). Four pairs of pygidial lobes. Of the paraphyses arising between the 2nd and 3rd lobes the middle paraphysis of the three is much the longest *phenax* Cockerell.
- Three pairs of lobes. Between the 2nd and 3rd lobes the paraphysis arising from the outer angle of the base of the 2nd lobe is much longer than the others *chrysobalani* Leonardi.

Ferris (1941, *Microentomology* 6:41) states that *Aspidiotus ceardi* Balachowsky which occurs in Algeria, Morocco and the Sahara is "apparently a *Melanaspis*." The original description and figures of this species given by Balachowsky give no indication of the presence of the paraphyses which are normally so conspicuously developed in this genus. For this reason, and because no specimens have been available for examination, it has not been included in the above key. Balachowsky described it as a *Hemiberlesia*, but it certainly does not appear to belong to that genus as at present understood.

Dentaspis rugosa sp. n. (fig. 5).

Scale of adult female white, so highly convex as to be almost globular but somewhat compressed laterally. Secretory appendix with regular transverse corrugations and of a felted, rather soft, nature. Larval exuvia golden, nymphal exuvia very pale. Ventral scale persisting round the margin in the anterior region.

Male scale white, parallel-sided, with golden exuvia, uncarinated.

Length of scale of adult female, 1.2-1.4 mm.; breadth, 0.8 mm.; height, 0.8 mm.

Specimens crowded together into an almost unbroken mass.

Body of adult female broadly pyriform in outline, sharply narrowed anteriorly, globose and membranous. Mouthparts situated unusually close to the anterior margin. Spiracles situated in shallow pits with about 10 parastigmatic glands associated with the anterior pair. Abdominal segmentation not clearly demarked. Pygidium very flatly rounded. Median lobes small, short and broad with serrated apices, widely set apart. Second lobes duplex, of the same form, but the outer lobule very indistinctly represented. Gland spines rather unusually short and stout, one just anterior to the median and to the second lobes



FIG. 5.—*Dentaspis rugosa* sp. n.: A, Dorsal and side views of scale of adult female; B, Adult female under pressure on slide; C, Pygidium; D, Antenna of larva.

and a group of two or three towards the base of the pygidium. Setae, gland spines or marginal pores between the median lobes absent. Marginal pores of the same size as the dorsal pores. Dorsal pores with short ducts scattered over the pygidium. Groups of pores occur in the marginal area of segments as far as the mesothorax and small groups of gland tubercles ventrally as far as the posterior spiracles. Perivulvar pores in five groups—median, 2-4; anterior laterals, 4-8; posterior laterals, 5-7 (average of 10 examples 3:6:6). Anal orifice nearer the base than the apex of the pygidium.

On twigs and undersurface of leaves of an unknown host plant. UGANDA (*G. H. E. Hopkins*), -i.31.

This species is closely related to *Chionaspis substriata* Newstead, which was made the type of a new genus *Dentaspis* by MacGillivray. *D. substriata* was described from specimens on palms from Uganda. Material has also been seen from Lake Kivu, Belgian Congo, on date palms, collected by T. D. A. Cockerell in 1931. *D. rugosa* differs from *substriata* in having five groups of perivulvar pores, gland spines of the pygidial fringe of a different form, more numerous dorsal pores, and the median lobes being more widely set apart. It also resembles *Chionaspis globosus* Brain in many respects but the scale is quite different.

D. rugosa is an extremely difficult species of which to get a microscopic preparation showing the pygidial fringe satisfactorily, owing to the extremely delicate nature of the dermis and globose form of the body.

***Duplachionaspis ugandae* sp. n. (fig. 6).**

Scale of adult female creamy white, moderately convex and apparently much broadened posteriorly although the true shape is not very clear as the individuals are crowded together just below the nodes of the grass; texture of scale thin with faint transverse striations but the outline of the sublying female does not show through. Exuviae very pale to pale brown



FIG. 6.—*Duplachionaspis ugandae* sp. n.: A, Adult female; B, Pygidium; C, Anterior spiracle.

and usually masked by a thin film of white secretory matter. Ventral scale thin, white and entire, except for a small hole anteriorly in some individuals, the young apparently escaping posteriorly through one or more small marginal slits between the dorsal and ventral scales.

Male scale small, white, parallel-sided, uncarinated, with pale brown exuvia.

Body of adult female fusiform with sclerotisation confined to the pygidial region. Pygidium broadly rounded, lobes relatively small and inconspicuous; median pair not yoked at their bases, broader than long with inner margins divergent and lacking notches, separated by a distance rather greater than half the width of one; second pair duplex, the inner lobule larger than the outer, of the same form as the median lobes but smaller and less conspicuous; some specimens show indications of a third pair but these are usually very inconspicuous. Four pairs of gland spines in the usual positions, one of each pair tending to be slightly larger than the other, and a group of about four at the base of the pygidium. No gland spines are present between the median lobes. Dorsal ducts in well-defined rows on the 3rd to 6th segments both inclusive, on the 6th segment the series is confined to a submedian row of usually 4 with 2 marginally. Ventral dermis of the pygidium with relatively numerous microducts and a submarginal row of somewhat enlarged setae. Perivulvar pores in five groups, median, 12-26; anterior laterals, 27-52; posterior laterals, 20-48 (average of 15 examples 20:41:38). Marginal groups of pores of variable sizes, including micropores, not occurring anterior to the second abdominal segment and gland tubercles not anterior to the third abdominal segment. Anterior spiracles with a rather large compact group of about 30 parastigmatic glands, posterior spiracles with a similar but rather smaller group of about 20.

In the vicinity of the nodes of an unidentified grass. UGANDA: Kampala (*H. Hargreaves*), 20.xi.26.

This species differs from *Duplachionaspis* MacGillivray as represented by its type species *graminis* Green, and other species referred to the genus by Ferris, in the nature of the pygidial lobes, which are squat and relatively inconspicuous. In other respects it conforms to the characters of the genus.

***Phenacaspis bauhiniæ* sp. n. (fig. 7).**

Scale of adult female silvery white, low convex broadened posteriorly. Exuviae pale golden. Ventral scale thin but entire except towards the posterior extremity.

Male scale, white, uncarinated.

Length of scale of adult female, 2.5 mm.; breadth, 1.3 mm.

Body of adult female fusiform membranous except for the pygidial region, and only showing very slight traces of sclerotisation when fully matured. Antennal tubercle with a long curved seta which is bifid at the base. Median lobes broader than long with inner edges divergent and apically serrate, separated by a distance of about the width of one and definitely yoked together at their bases. Second lobes duplex, the inner lobule being much larger than the outer and flatly rounded. Gland spines of normal form occur singly, four on either side, one between the median and second lobes, one just anterior to the second lobes and the other two at widely spaced intervals anterior to this. Marginal and submarginal pores with short stout ducts and the capitate head carrying a long microduct. Dorsal pores similar to the marginal pores but the long microduct on the capitate head replaced by the normal club-shaped process. Dorsal pores in definite series as far as the 6th segment. Marginal areas of segments with scattered pores as far as the mesothoracic region and groups of gland tubercles ventrally as far as the anterior spiracles. Perivulvar pores in five groups, median, 2-9; anterior laterals, 12-21; posterior laterals, 12-26 (average of 17 examples 6:15:19). Anal orifice situated towards the base of the pygidium.

On leaves of *Bauhinia rufescens* (Leguminosae). SENEGAL: M'Bambey (*J. Risbec*), 1944. Material preserved in formalin.

P. bauhiniæ is closely related to *Chionaspis nigerensis* Vayssière described from the Upper Niger on *Ximenia americana* but the median lobes are of different shape and more closely set together, and the dorsal and perivulvar pores are

less numerous. It is also closely related to *Chionaspis usambarica* Lindinger but has much shorter pygidial plates. It differs from *Chionaspis carpenteri* Laing in having smaller and very much less prominent lateral lobes.

The long slender microducts carried by the capitate heads of the marginal pygidial pores, which are so clearly seen in *bauhiniae*, are also plainly visible



FIG. 7.—*Phenacaspis bauhiniae* sp. n.: A, Adult female; B, Pygidium.

in *nigerensis*. Traces of similar microducts have been seen in other species, notably *P. visci* var. *umtali* Hall, *Chionaspis sinoiae* Hall, *P. whitehilli* Hall and *P. lounsburyi* Cooley.

It is doubtful if this species is correctly placed but it will serve until a revision of the genus *Phenacaspis* Cooley & Cockerell is undertaken.

Phenacaspis kenyae sp. n. (fig. 8).

Scale of adult female white, low convex, so much broadened as to be subcircular with exuviae extending beyond the margin; texture thin, with the sublying female faintly discernible; exuviae pale brown masked by a thin film of white secretory matter. Ventral scale thin, white, in some individuals remaining adherent to the host plant, in others coming away partially, whilst in others it comes away entire.

Male scale white, parallel-sided, uncarinated, with yellow or very pale brown exuvia.

Diameter of scale of adult female, 2.5 mm.

Body of adult female membranous except for the pygidial region, fusiform, broadest in the mesothoracic region. Pygidium rounded with two pairs of lobes; the median pair with their bases yoked, divergent, with inner edge longer than the outer, rounded at the apex and not notched or serrated, separated by a definite U-shaped notch about two-thirds the width of one of the lobes; the second lobes duplex, the inner lobule much larger than the outer, of the same general shape as the median lobes but smaller. Gland spines not present between the median lobes but a pair in each interlobular space. In these pairs one is always rather longer than the other; anterior to these is a group of three of varying sizes, and at the base of the pygidium there is a group of 6-8 spines. Dorsal pores in well-defined

rows, the submarginal and submedian groups being separated and not continuous; they occur from the 3rd to the 6th segments, both inclusive. On the 6th segment the submedian group is represented usually by three pores and the submarginal group by two. Ventral dermis with a few microducts arranged in three series running in from the margin with a scattered group submarginally at the base of the pygidium. Groups of pores, microducts and gland tubercles are found in the marginal area of the 2nd and 3rd abdominal segments.

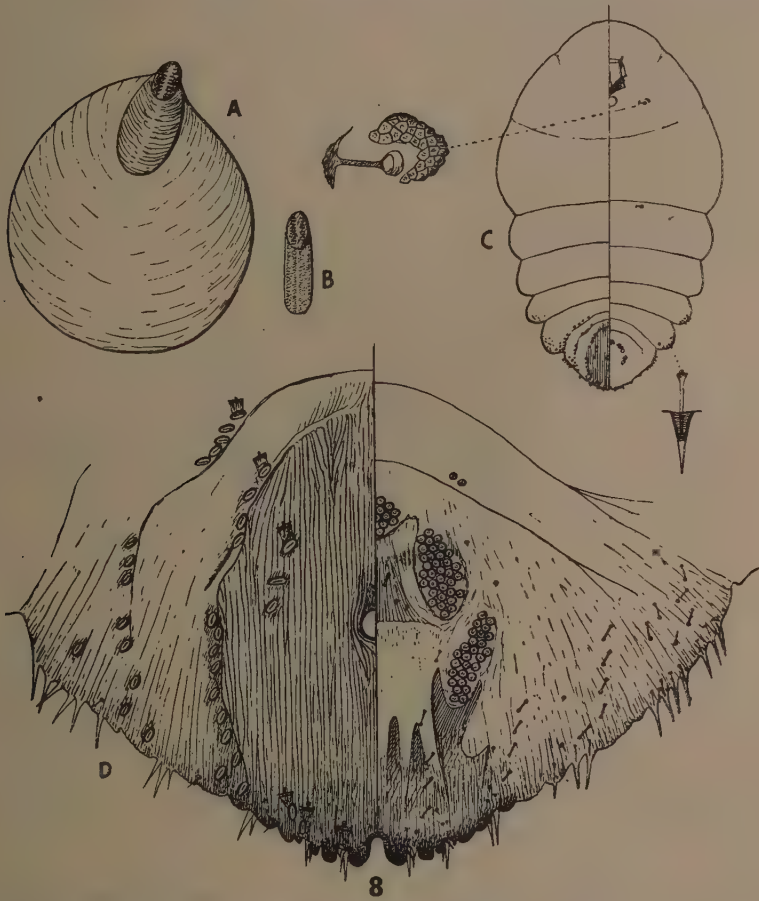


FIG. 8.—*Phenacaspis kenyae* sp. n.: A, Scale of adult female; B, Male scale; C, Adult female; D, Pygidium.

Anal orifice situated near the centre of the pygidium. Perivulvar pores in five groups, median, 11–25; anterior laterals, 22–44; posterior laterals, 16–37 (average of 22 examples, 18 : 34 : 27). Thirteen examples showed signs of supplementary groups of perivulvar pores, in all but three of these only one group of 1–4 pores was represented, in the other three, two groups, the median and one or other of the anterior lateral groups, were represented by 1–4 pores. A crowded group of some 30 parastigmatic glands associated with the anterior spiracles and a similar but smaller group of about 15 with the posterior spiracles.

On an unknown species of a Gramineous plant, chiefly in the vicinity of the nodes, above and below, with some specimens also at the bases of the leaf sheaths. KENYA (*F. B. Notley*), 3.iv.36.

Indications of three groups of pores on the preceding segment to that carrying the normal five groups of perivulvar pores suggests that this species might be assigned to the genus *Poliaspis* Maskell. The supplementary groups, however, were only present in 50 per cent. of the examples and in no example were more than two groups present. Those examples in which supplementary groups of pores are present might be assigned to *Poliaspis*, those in which they are lacking to *Phenacaspis*. *P. kenyae* differs from both *Phenacaspis* and *Poliaspis* in having the interlobular gland spines in pairs. For the time being it is placed in the genus *Phenacaspis* until such time as a revision of the African species of this and other allied genera is undertaken.

The nature of the scale of *P. kenyae* is reminiscent of that of *P. dilatata* Green but the microscopic characters of the adult female differ in the lack of serrations on the inner surfaces of the median lobes, the greater number of the perivulvar pores and the presence of pairs of gland spines in the interlobular spaces (except between the median pair of lobes).

***Phenacaspis whitehilli* sp. n. (fig. 9).**

Scale of adult female long, convex, only moderately broadened posteriorly and opaque waxy white. Exuviae pale brown covered by a thin film of white secretory matter. Ventral scale persistent except at the posterior extremity and along a median channel.

Male scales small, parallel-sided, non-carinated, with pale brown exuvia; they occur in large clusters, not lying flat on the host plant but tilted very nearly vertically.

Length of scale of adult female, 4–5 mm.; breadth, 1.25–1.5 mm.

Body of adult female fusiform; in young adult females the body is relatively narrower with roughly parallel sides. Old individuals showing slight sclerotisation of the tissues as far as the 1st or 2nd abdominal segment. Ventral dermis posterior to the anterior spiracles and between the lines joining the anterior and posterior spiracles with scattered minute pyramidal spines. Pygidium broadly rounded. Median lobes rather prominent, slightly divergent, rounded apically, with bases clearly yoked but separated by a distinct median notch. Second lobes duplex with the inner lobule relatively long and narrow. Gland spines rather long, arranged as shown in fig. 9, D. A single marginal pore between the median and second lobes and a group of usually four marginally of the 6th abdominal segment. Capitate heads of marginal pores carrying relatively long minute ducts; these are not as long or as conspicuous as those found in *P. baubiniæ*. Dorsal ducts in well-defined segmentally arranged series. On the 6th segment there is a break between the submedian series and small submarginal group; on the 5th the submedian and submarginal series are practically continuous. The series are continuous on the 1st to 4th segments and in the case of the 2nd and 3rd segments they are continuous from margin to margin. Marginal groups of scattered pores occur as far as the mesothorax. Small groups of gland tubercles of normal form ventrally on each segment as far as the anterior spiracles. Perivulvar pores in 5 groups, median, 1–11; anterior laterals, 17–31; posterior laterals, 28–56 (average of 15 examples 7 : 23 : 41). Anterior spiracles with a small group of about 7 parastigmatic glands. Anal orifice situated towards the base of the pygidium.

On *Euphorbia* sp., UNION OF SOUTH AFRICA: Cape Province, Whitehill (*T. D. A. Cockerell*), 26.xi.31.

Brain (1919, *Bull. ent. Res.* 9) described *Chionaspis euphorbiae* (: 234) and *C. globosus* (: 236) both from *Euphorbia* from South Africa. Neither of these species is correctly placed in the genus *Chionaspis* but neither do they belong



FIG. 9.—*Phenacaspis whitehilli* sp. n. : A, Scale of adult female; B, Male scale; C, Body; D, Pygidium. *Phenacaspis lounsburyi* Cooley; E, Pygidium of adult female.

to the genus *Phenacaspis* and they are clearly unlike *P. whitehilli*. No other species of *Chionaspis* or allied genera seem to have been recorded on *Euphorbia* from the African continent.

P. whitehilli comes closest to *P. lounsburyi* var. *ekebergiae* Brain, but unfortunately neither the type nor any authentic material has been available for comparison. *P. l.* var. *ekebergiae* was described by Brain (1920, *Bull. ent. Res.* 10: 99) on *Ekebergia* sp. (Meliaceae) from Durban, a very different host plant and locality. The figure given by Brain suggests that the median lobes are finely serrated and the perivulvar pores somewhat less numerous. The pygidium of *lounsburyi* Cooley is markedly smaller than that of *whitehilli* and one assumes the same to be the case in the var. *ekebergiae* or it would have been noted. For these reasons *whitehilli* has been treated as a new species.

The comparative prominence of the median and second lobes of *whitehilli* is not typical of the genus *Phenacaspis*, but there are several African and Indian species which exhibit this characteristic to a greater or lesser degree.

The opportunity is here taken to make a few remarks on *P. lounsburyi* Cooley and to give a figure of the pygidium (fig. 9, E) for comparison with *whitehilli*. It will be noticed that in both cases the capitate heads of the marginal pores carry long ducts; these are neither so long nor so conspicuous as those found in *P. bauhiniae*.

Small portions of three separate lots of material labelled *P. lounsburyi* Cooley from the collections of the Department of Entomology, Pretoria, were very kindly made available by Dr. T. J. Naudé, Chief of the Department. I am much indebted to him and to Mr. H. K. Munro for looking out and forwarding this authentic material.

The details supplied with the three lots were as follows:—

1. Ac. C. 1249 (probably Brain's No. 170), Ceres, C.P., 1896 (*C. P. Lounsbury*). "On *Rhus thunbergi* and other plants. Common. Stains some foliage red."
2. No. 166 (Brain). On native plant (Proteaceae), Wolseley, Cape, June 1915 (*C.P.L.*).
3. No. 185 (Brain). Kluitjeskraal, Wolseley, Cape, 3.ii.15 (*J. W. Hodgson*). On reed-grass.

The first two mentioned were recorded by Brain under *P. lounsburyi* Cooley (1920, *Bull. ent. Res.* 10: 99), a species which was described by Cooley (1898, *Canad. Ent.* 30: 87) from material on an unidentified plant from Ceres sent by Lounsbury. It is, therefore, quite possible that Ac. C. 1249 represents part of the type material.

The three lots of material of *lounsburyi* show some variation but the specimens all differ from *whitehilli* in being smaller. The pygidia of the two species drawn to the same scale are shown in fig. 9, E. In every individual of *lounsburyi* examined the median lobes have a finely but clearly serrated margin. The perivulvar pores and dorsal pores are less numerous than in *whitehilli*.

Comparison of certain characters in *whitehilli* and the three lots of *lounsburyi* material and *lounsburyi* var. *ekebergiae* as described is made in the table on page 71.

It will be noticed that there is a certain amount of variation in the three lots of *lounsburyi* material but there are no grounds for not believing that they are one and the same species. *P. whitehilli* comes closest to the Ac. C. 1249 lot of material of *P. lounsburyi*.

	Parastigmatic glands to anterior spiracles	Perivulvar Pores			No. of dorsal pores in sub-median series on Segment VI.
		Med.	Ant. lat.	Post. lat.	
Ac. C. 1249. . . .	9 (10)	4 (9)	14 (9)	27 (9)	8 (10)
No. 166	4 (14)	6 (12)	15 (12)	22 (11)	4 (14)
No. 185	4 (6)	6 (5)	13 (5)	22 (7)	4 (7)
<i>P. lounsburyi</i> var. <i>ekbergiae</i>	—	6-9	11-20	29-46	9
<i>P. whitehilli</i> . . .	7 (21)	7 (15)	23 (15)	41 (15)	11 (25)

The number of individuals from which the averages were calculated is given in brackets.

Scleromytilus gen. n.

Belonging to the tribe Diaspidini of the family DIASPIDIDAE. Body elongate with the entire thoracic region and first abdominal segment very strongly sclerotised. Median lobes large and conspicuous, not zygotic and with a pair of small flat apically bifurcate gland spines between. No traces of other lobes. Gland spines in four groups of 2 to 4 spines between the median lobes and base of the pygidium; the spines are of two kinds: one the simple pointed type, the other narrow, flattened with bifurcate tip. Dorsal pores relatively small with relatively short ducts, occurring in irregularly defined series as far as the 7th segment. The series become less well defined and almost indistinguishable towards the 7th segment. Perivulvar pores wanting. Lateral projections of free abdominal segments with a deep indentation, the anterior being larger than the posterior section. Anal orifice towards the base of the pygidium. No spurs or sclerotic bosses present on any abdominal segment. Scale of the female white, elongate, very highly convex with exuviae terminal, ventral scale entire, white, thin but tough. Scale of male of more or less similar form and colour but narrower and flatter, uncarinated.

Genotype:—*Scleromytilus hargreavesi* sp. n.

The affinities of this genus are not clear. In the nature of the lateral margins of the free abdominal segments it bears some resemblance to *Phaulomytilus* Leonardi, but the pygidial characters bear no resemblance to that genus. It appears to bear some relationship to *Aonidomytilus* Leonardi, from which it differs in having a single pair of lobes, the presence of perivulvar pores, marginal and dorsal ducts of much the same size and the conspicuous indentation of the lateral projections of the margins of the free abdominal segments. It is probably closest to *Mitulaspis* MacGillivray, a genus which was erected for the reception of another species from Uganda, despite the obvious difference in the shape and number of the pygidial lobes and the character of the lateral projections of the free abdominal segments.

Scleromytilus hargreavesi sp. n. (fig. 10).

Scale of adult female pyriform, off white, with faint transverse striations, very highly convex and hemispherical in side view. Larval exuvia terracotta, nymphal exuvia brown. The scale is very tough, rendering it far from easy to extract the highly sclerotised female without damage. Ventral scale entire, white, thin but tough.

Male scale pale brown with terracotta exuvia, uncarinated and of more or less similar form and colour to that of the female but narrower and flatter.

Length of adult female scale, 1.5-2.0 mm.; breadth, 0.8 mm.; height, 0.8-1.0 mm.

Adult female at maturity with the entire thoracic region and 1st abdominal segment very

strongly sclerotised, 2nd, 3rd and 4th abdominal segments membranous but with lateral marginal projections somewhat sclerotised, pygidium with a sclerotic pattern. Antennae consisting of a flat tubercle carrying about 6 stout setae of approximately equal length.

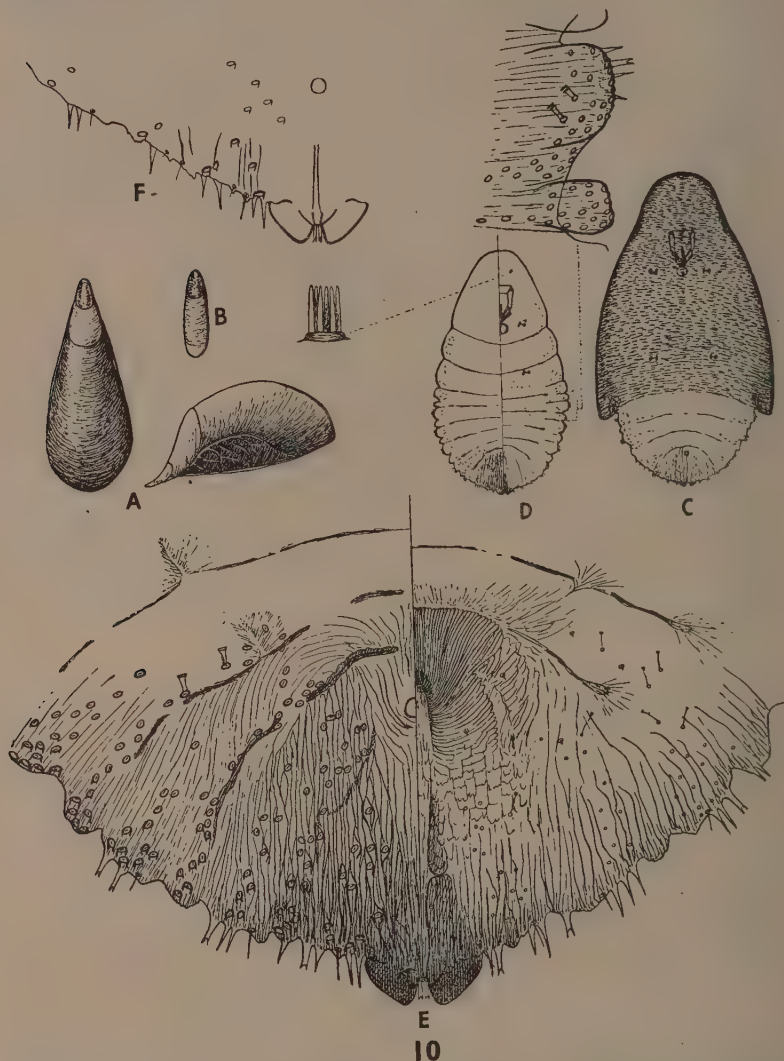


FIG. 10.—*Scleromytilus hargreavesi* sp. n.: A, Dorsal and side views of scale of adult female; B, Scale of male; C, Fully matured adult female under pressure on slide; D, Early adult female; E, Pygidium; F, Pygidium of second stage female.

Lateral margins of free abdominal segments produced, but each with a deep indentation dividing it into a wider projection anteriorly and a narrower one posteriorly. Pygidium broadly rounded with a conspicuous pair of median lobes; these are large, acutely rounded,

with the outer edge falling away sharply, very like those of *Andaspis hawaiiensis* (Maskell) in shape; they are separated by a distance of about one-quarter the width of one. Other lobes wanting. Two very small gland spines occur between the median lobes; these are plate-like, of more or less uniform width throughout, and bifurcate at the apex. Four groups of gland spines occur between the median lobes and base of the pygidium on either side, each group consists of two or three spines which are of two types, one the typical pointed gland spine, the other a broad more or less parallel-sided plate-like structure with bifurcated tip. Dorsal pores relatively small, occurring as far as the 7th segment, scattered or in very ill-defined series. Ventral dermis in the median area with a faintly tiled ornamentation. Anal orifice situated towards the base of the pygidium. Perivulvar pores wanting. Margin of abdominal and thoracic segments with scattered pores but gland tubercles not present anterior to the second free abdominal segment. Anterior spiracles with a group of some 7 parastigmatic glands and posterior pair with usually two.

On small twigs of *Loranthus* sp., UGANDA: Kampala (*H. Hargreaves*), 3.vii.29.

Specimen selected as "type" is a young adult female in which the sclerotisation of the thoracic region has not yet developed. In fully mature specimens the thoracic region is broadly oval in cross section and being strongly sclerotised of necessity becomes broken when mounted.

Vol. 97. Part 4. Pp. 75-115, 36 figs.

22nd July, 1946.

THE
IMP. INST. LIBRARY
13 AUG 1946
SERIAL Eu. 344
SEPARATE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

X CROWSON, R. A., B.Sc., A.R.C.S., D.I.C., F.R.E.S.

A revision of the genera of the Chrysomelid group

SAGRINAE (Coleoptera) 75-115, 36 figs.

PAGE

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 12s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.
C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.
H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Registrar :

Finance and House Committee.

G. FOX-WILSON, N.D.H. (Chairman).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (Chairman).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (Chairman).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (Secretary).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (Chairman).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

A REVISION OF THE GENERA OF THE CHRYSOMELID GROUP SAGRINAE (COLEOPTERA)

By R. A. CROWSON, B.Sc., A.R.C.S., D.I.C., F.R.E.S.

Manuscript received 21st February, 1945.

(Read 16th January, 1946.)

WITH 36 TEXT-FIGURES.

INTRODUCTORY.

THE division Eupoda of the family CHRYSOMELIDAE is commonly defined by the absence of the side edges to the prothorax, and the eyes being normally not in contact with the front of the prothorax; some authors would add "front coxae more or less projecting, separated by a narrow process of the prosternum, their cavities completely closed behind." Thus defined, the group will include the subfamilies SAGRINAE, ORSODACNINAE, DONACINAE, CRIOCERINAE, MEGALOPODINAE, and MEGASCELINAE of the normal classification. The last two subfamilies mentioned are, however, usually excluded; to do this the definition must be extended as follows:—"Antennae moderately long, never shorter than the head and prothorax together, very rarely serrate. First visible abdominal sternite with the antero-lateral angles not evidently prolonged outside the met-episterna, the intermediate abdominal sternites not narrowed in the middle line. Eyes not sharply emarginate." The subfamilies excluded thus are generally referred to the Camptosomata on account of their abdominal structure and in the case of the MEGALOPODINAE their short serrate antennae. But in several important characters the latter group are closer to the SAGRINAE than are the DONACINAE or CRIOCERINAE—notable among these are the structure of the labium (see Chapuis 1874), of the aedeagus (Chen 1940), of the wings (*id.*), and of the met-endosternite (Crowson 1938, 1944). However, I do not propose to consider them here, chiefly because the British Museum material of the group is not at present accessible. The DONACINAE include 3 main genera, species of all of which occur in Europe, hence the group is dealt with adequately in works on European Coleoptera. The CRIOCERINAE include two very large and difficult genera with a number of small rather heterogeneous ones; a revision of the genera in this group would be very desirable and I hope to be able to undertake it in the future. There remain the SAGRINAE and ORSODACNINAE, which might roughly be described as the respectively Southern and Northern representatives of the archaic CHRYSOMELIDAE. The two groups are rather intimately related, and it is quite possible that they could be included in a single subfamily, as was done by Lacordaire and Chapuis; I tentatively adopt this course here.¹

The chief character which these authors relied on to separate the present group from other CHRYSOMELIDAE was the presence of a well-developed bilobed ligula; this occurs also in MEGALOPODINAE but in no others of the present family although it is general in CERAMBYCIDAE and in BRUCHIDAE. The latter family, it can hardly be doubted, are a direct offshoot from the group under consideration and like the MEGALOPODINAE ought logically to be con-

¹ I now consider it better (May 1946) to keep the subfamilies separate.—R.A.C.
TRANS. R. ENT. SOC. LOND. 97. PART 4. (JULY 1946.) E

sidered with them. However, the BRUCHIDAE have already been dealt with generally by Bridwell (1932) and I am excluding them from the present study. I must now try to formulate a strict definition for the SAGRINAE-ORSODACNINAE group. The most difficult group to exclude in a definition is the CERAMBYCIDAE, although I do not consider that the relationship of SAGRINAE-ORSODACNINAE to them is so close as it is to BRUCHIDAE and the rest of the CHRYSOMELIDAE.

Definition of the group SAGRINAE-ORSODACNINAE.

Antennae always at least as long as the head and prothorax together, never clubbed and very rarely slightly serrate (if more than half as long as the body the first visible abdominal sternite as long as the rest together and the tibiae lack spurs, except *Cucujopsis*), inserted at the sides of the front before the eyes, not capable of being bent horizontally backwards over the dorsum. Eyes entire (or if slightly emarginate, tibiae without spurs, except *Zeugophora*), distinctly separated from the front of the prothorax in the normal position of the head, the latter without an evident median longitudinal line. Mentum not pedunculate, ligula well developed (fig. 5) and more or less deeply bilobed, gular sutures never confluent. Prothorax usually more or less distinctly narrower than the elytra, sharply defined lateral margins rarely present, without a transverse constriction just before the base. Front coxal cavities closed behind (except in *Syneta*), the pleural processes not fused to the prosternal process, the latter narrow between the coxae which are more or less projecting and have evident trochantins (fig. 26). Metasternum with a transverse suture on each side bounding a narrow sclerite just in front of the coxa (figs. 24-26, SS). Tibiae with or without apical spurs, if with, tarsal claws usually split or appendiculate. Tarsi without empodia. Hind femora often more or less inflated but never with the internal sclerite characteristic of the HALTICINAE. Elytra never sharply truncate, rarely leaving the pygidium exposed and rarely with definite striae or rows of punctures. Wings usually with complex anal venation (figs. 9-15), usually 4 or more distinct anal veins, without a dark patch below apex of vein Cu. Metacoxae nearly contiguous, met-endosternite with a narrow stalk, no median projection, separated anterior tendons, and the lateral parts of the ventral process strongly differentiated (fig. 23). Visible abdominal sternites 5, the antero-lateral angles of the first normally not prolonged anteriorly outside the metepimera. Aedeagus with lateral lobes (parameres) differentiated except in *Aulacoscelis* and *Syneta*, with or without internal struts. Female genitalia: ovipositor elongate, with baculi and coxites bearing movable styli (Orsodacnini), or short with reduced coxites (*Polyoptilus*).

Larvae as far as known (*Sagra*, *Orsodacne*, *Syneta*, *Zeugophora*) internal feeding with legs short or absent, but not cylindrical wood-borers. Larval mandibles with a fairly straight cutting edge and a single tooth at the apex, without a mola.

The above definition excludes the BRUCHIDAE (including *Rhaebus*) by the structure of the mentum, the CURCULIONOIDEA by the structure of the gula, the MEGALOPODINAE by the structure of the antennae, the abdomen and the absence of the empodium, the remainder of the CHRYSOMELIDAE by the structure of the ligula and head; the CERAMBYCIDAE are fairly well excluded by the first two sentences of the adult definition taken together, and more satisfactorily by the larval structure.

On certain genera excluded from the SAGRINAE.

The genus *Cheiloxena* Baly (1860), with 2 Australian species, was included in SAGRIDAE by its describer and by all more recent authors who have dealt

with it (Chapuis, Blackburn, Jacoby, Weise). In spite of this, I am fairly certain that it does not belong in this group but probably may be included in the EUMOLPINAE. The most prominent feature of the forms I am considering—the large bilobed ligula—is entirely lacking in *Cheilozena*, which is also aberrant in the structure of the upper surface of the head (in which it resembles EUMOLPINAE), in the bifid apices of the mandibles (also a feature of EUMOLPINAE), the split tarsal claws, in having the lower lobe of the third tarsal joint slightly emarginate (as in CHRYSOMELINAE) instead of deeply bilobed, in the wing venation (fig. 15) which is much like that of the African Eumolpine *Euryope* (note the dark patch below the apex of Cu), in the aedeagus which from an imperfect dry preparation seems to have a reduced tegmen as in the more advanced CHRYSOMELIDAE generally, and finally in general appearance.

Two other genera referred to the SAGRINAE by Chapuis (1873) are *Rhaebus* Fisch. de W. and *Eubaptus* Chevrolat, both of which in my opinion are unquestionably Bruchids. The most recent authority on BRUCHIDAE, Bridwell, includes *Eubaptus* with that family (in a separate subfamily) and summarises its characters (1932), so it does not seem necessary to deal with it here. The genus *Rhaebus* is, however, not accepted as Bruchid by Bridwell (who states that he has not actually seen the insect). *Rhaebus*, if it is included in the CHRYSOMELIDAE at all, would have to be included in the group under consideration on account of the large bilobed ligula. So it seems necessary to summarise my reasons for disagreeing with Bridwell's conclusion. In the first place, the basic character usually given to separate BRUCHIDAE from CHRYSOMELIDAE is the structure of the mentum, which is usually described as pedunculate in the former family; in *Rhaebus* the mentum is essentially similar to that of normal BRUCHIDAE, though appearing a little different in correlation with the smaller eyes. Secondly, there is another structural feature in which the BRUCHIDAE differ sharply from the SAGRINAE and their allies—the met-endosternite (Crowson 1938, 1945). I have investigated this organ in *Rhaebus* and find it to be essentially Bruchid. Thirdly, the adults of *Rhaebus gebleri* are recorded as emerging from the seeds of the plant *Nitraria schoberi*. Finally, there are a number of minor characters in which *Rhaebus* resembles various Bruchids: the deeply emarginate eyes, the truncate elytra with regular rows of punctures, the prosternal process evanescent between the front coxae, the peculiar tarsal claws, the hind tibiae possessing large and specialised apical spurs, etc.

The Neotropical region is peculiarly rich in Chrysomelid forms which are difficult to classify—as for example the MEGASCELINAE, *Aulacoscelis*, *Hornibius*, *Plastorsodacne*, *Psatyrocerus*, and *Stenomela*. Of these, the MEGASCELINAE belong, in my opinion, with the Camptosomata, the genus *Stenomela* (*Apocinocera*) has not been available to me for study, the position of *Aulacoscelis* is discussed below, and *Hornibius* is dealt with in the systematic part of this paper. There remains *Psatyrocerus* Blanchard, which has usually been attributed to the CRIOCERINAE (in company, be it noted, with *Syneta* and *Zeugophora*), and with which Brèthes places his *Plastorsodacne*; the possibility must be considered that *Psatyrocerus* might belong with the forms I am studying. The most characteristic feature of the present group—the large bilobed ligula—is scarcely to be recognised in *Psatyrocerus*, but it is to be remembered that it is poorly developed also in *Syneta* and *Hornibius*; the former genus has bifid tarsal claws similar to those of *Psatyrocerus*. But the latter genus differs from all the Orsodacnini (except *Syneta* subg. *Tricolema*)

in the absence of tibial spurs on all the legs. This suggests a comparison with the Sagrini, but *Psatyrocerus* has none of the other leading characters of that group, such as the inflated hind femora, the long 1st abdominal sternite, the crossed grooves on the frons, and the simple tarsal claws. The antennae of *Psatyrocerus* are inserted differently from those of any SAGRINAE that I know, but rather similarly to those of many EUMOLPINAE; there is a median longitudinal groove on the head (not known in any SAGRINAE), and the trochanters have their junction with the femora in a plane practically at right angles to their longitudinal axis, more or less as in the Curculionid genus *Apion*—this too is a character I have not seen in SAGRINAE. In view of these facts, and of the anomalous metendosternite of *Psatyrocerus* sp. (fig. 21), I am excluding the genus from the subfamily SAGRINAE.

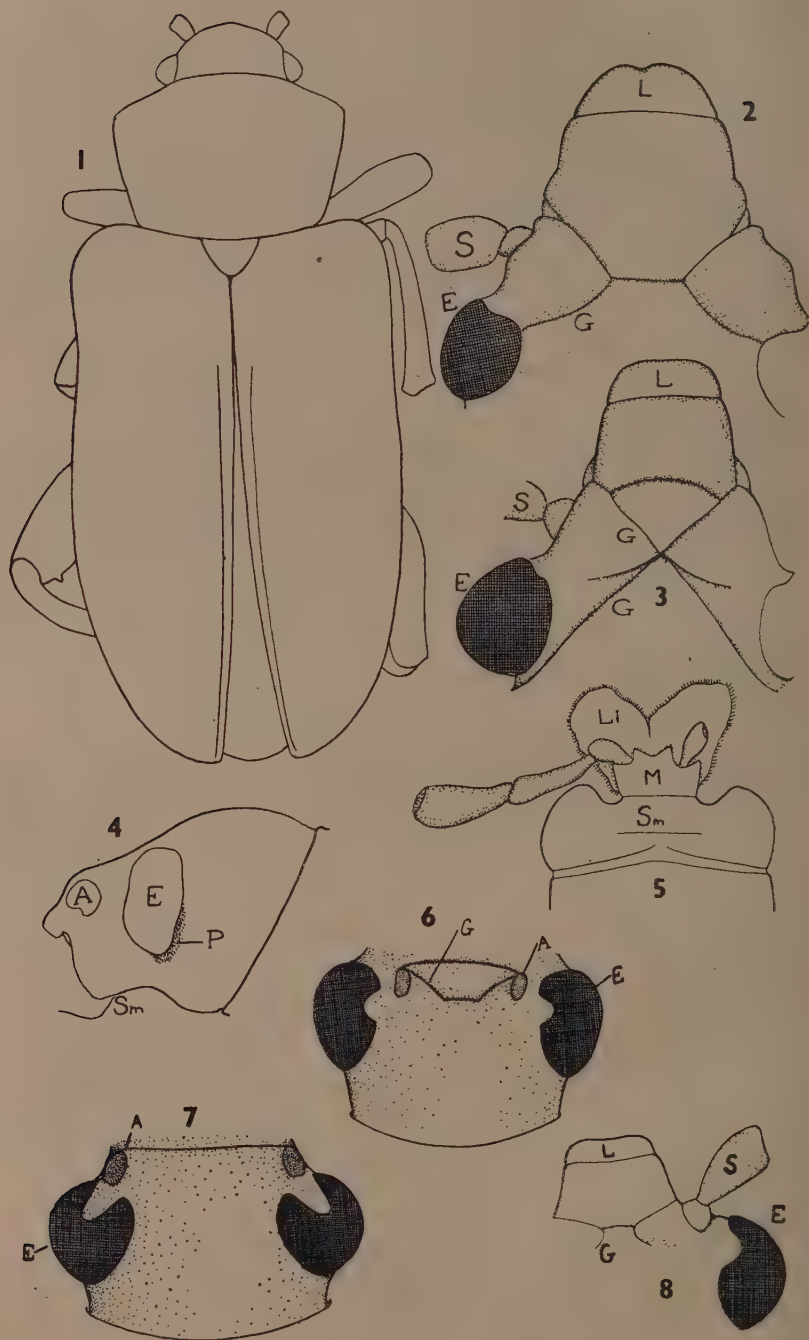
On the systematic position of *Aulacoscelis* Chevrolat.

The Mexican genus *Aulacoscelis* was referred to the CHRYSOMELINAE by its describer, but transferred to the SAGRINAE by Chapuis, chiefly on account of its large bilobed ligula. Jacoby followed Chapuis in the *Biologia Centrali-Americana* but changed his opinion in *Genera Insectorum*. Maulik has stated that "*Aulacoscelis* . . . cannot be included in the SAGRINAE at all" (1941), but he is using the term SAGRINAE in a restricted sense, excluding the Orsodacnini (but apparently including *Cheiloxena*). In my opinion *Aulacoscelis* must be included in the SAGRINAE *sensu lato* on account of the characteristic form of the ligula and the met-endosternite, and the essentially Eupodan form of the head and coxal cavities. It has, however, significant resemblances to the CHRYSOMELINAE in the only shallowly bilobed third tarsal joint, the wing venation, and the aedeagus (which much resembles that of *Timarcha*—cf. Sharp and Muir 1912). The SAGRINAE are probably the basic group of the CHRYSOMELIDAE, from which all the others must directly or indirectly have arisen, hence it is not surprising that between these groups and the SAGRINAE there exist a certain number of annectant forms. Such, for instance, is the genus *Aulacoscelis* in relation to the CHRYSOMELINAE; possibly *Cheiloxena* to the EUMOLPINAE, *Ametalla* to the DONACIINAE, and MEGALOPODINAE to the Camptosomata—even perhaps *Rhaebus* to the BRUCHIDAE. The boundaries separating the SAGRINAE from the rest of the family must be drawn more or less arbitrarily, and I think the bilobed ligula forms as good a one as any character so far proposed. *Aulacoscelis*, though included in SAGRINAE, is evidently not nearly related to any of the genera of Sagrini, nor can it easily be included in Orsodacnini, so I think it must constitute a separate tribe Aulacoscelini.

Key to the Genera and Tribes of SAGRINAE.

1. Head with more or less triangular raised areas bounded by grooves inside the points of insertion of the antennae, the apices of the triangles commonly meeting and forming an X-shaped figure (fig. 3). Tibiae without evident spurs. 1st abdominal sternite in middle line about as long as rest together. Mesocoxae not at all projecting. Femora usually much thickened, especially in hind legs. Species usually large and stout, not occurring in Holarctic region (Sagrini s.str.) 8.
- Head without such distinct grooves; if such triangular areas are indicated their apices are widely separated (figs. 6-8). Tibiae with small but distinct spurs. 1st abdominal sternite in middle line shorter than rest together. Mesocoxae often more or less projecting. Femora not notably thickened. Species small, parallel-sided, slender 2.

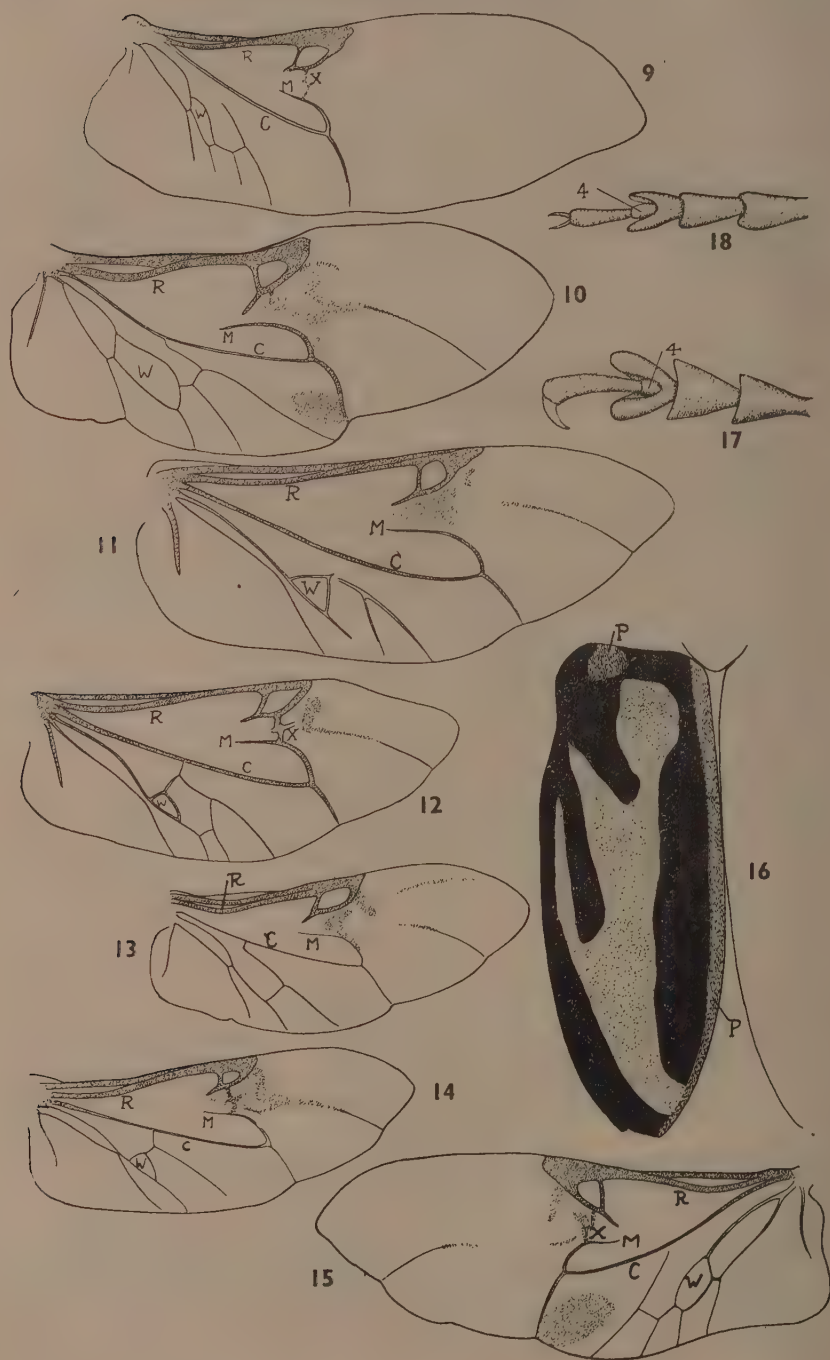
2. Prothorax with sharp and distinct side edges, tarsal claws simple . . . 3.
Prothorax without distinct side edges, often toothed at sides, tarsal claws usually toothed or appendiculate (*Orsodacnini*) . . . 4.
3. Eyes large, temples behind them short and not prominent, mandibles slender and acute. Prosternum long in front of coxae, hind angles of prothorax well marked, a short longitudinal impressed line on each side of pronotum close to base. Metepisterna not much broadened in front. Central America and Arizona. (*Aulacoscelini*) . . . *Aulacoscelis*.
Eyes small, temples behind them long and prominent, mandibles short, stout and sharply bent, clypeus emarginate in front. Prosternum very short in front of coxae, pronotum with hind angles obsolete, without longitudinal impressed lines. Metepisterna strongly broadened in front. Tierra del Fuego, Patagonia. (*Hornibiini*) . . . *Hornibius*.
4. Tarsal claws simple. Form rather flattened. Head large. Prothorax with several teeth at the sides. Head with traces of the triangular areas visible (fig. 8). Australia . . . *Cucujopsis*.
Tarsal claws split or appendiculate . . . 5.
5. Eyes smaller and less prominent, entire, temples prominent behind them. Prothorax with one or several more or less prominent teeth at the middle of each side. Procoxal cavities not fully closed behind. Tarsal claws appearing unequally bifid. Last abdominal sternite in ♀ deeply and hemispherically excavate. Holarctic . . . *Syneta* (*Tricolema* Crotch).
Eyes larger, more prominent, temples short and inconspicuous. If sides of prothorax toothed, eyes sharply emarginate. Procoxal cavities fully closed behind . . . 6.
6. Tarsal claws unequally bifid, divergent. Eyes entire, head prognathous. Sides of prothorax not toothed. Elytra without punctured striae. Holarctic, Chili (?) . . . *Orsodacne*.
Tarsal claws divaricate with large rounded appendices, procoxal cavities rounded, trochantins hidden . . . 7.
7. Eyes sharply emarginate, head more or less prognathous. Prothorax with sides bluntly toothed, prosternal process narrow. Elytra without punctured striae. Holarctic, Oriental, Ethiopian . . . *Zeugophora*.
Eyes entire, head sharply deflexed, hypognathous. Prothorax with sides not toothed, prosternal process broad between the coxae. Elytra with distinct punctured striae. Madagascar . . . *Hemydacne*.
8. Prothorax with front angles not produced into prominent tuberosities (cf. fig. 1) . . . 9.
Prothorax with front angles produced into prominent tuberosities (fig. 32). Not Australian . . . 19.
9. The apices of the inter-antennal triangles very distinctly separated, the grooves not forming an X-shaped figure; eyes coarsely faceted, less prominent (fig. 2). Hind femora strongly toothed. Australian . . . 10.
Apices of the inter-antennal triangles meeting, the grooves forming an X-shaped figure (fig. 3) . . . 11.
10. Prothorax with more or less distinct side-margins. Elytra without punctured striae. 4th tarsal joint about half as long as the lobes of the 3rd . . . *Duboulaia*.
Prothorax without distinct side margins. Elytra with more or less distinct punctured striae. 4th tarsal segment almost as long as lobes of 3rd (cf. fig. 18) . . . *Coolgardica*.
11. Hind femora not toothed below. 4th tarsal segment about half as long as the lobes of the 3rd. Mesosternal process reaching back to level of the hind borders of the coxal cavities. Pro- and mesosterna without tuberosities . . . 12.
Without these characters in combination; Australian . . . 13.



12. *Metepisterna* shallowly transversely impressed close to apex (fig. 24). Palpi with last joint securiform in the male, markedly broadened in the female. Pronotum finely sculptured, appearing more or less smooth with the naked eye, sides of prothorax markedly rounded. Australian *Megamerus*.
Metepisterna with a narrow apical raised area separated from the rest by a clearly marked line (as in fig. 25). Apical segment of palpi similar in both sexes, not notably broadened. Pronotum coarsely and rugosely sculptured, prothorax more or less parallel-sided. Madagascar. *Rhagiosoma*.
13. 4th tarsal segment at least two-thirds as long as the lobes of the 3rd (fig. 18); basal part of 3rd segment as long as its lobes. Mesosternal process reaching back almost to the level of the hind margins of the coxal cavities, narrow. Hind femora not much thickened, with or without a small tooth close to the apex. General form rather narrow 14.
 4th tarsal segment not more than half as long as the lobes of the 3rd (fig. 17); basal part of 3rd segment shorter than its lobes. Mesosternal process broader, usually not reaching as far back as hind margins of middle coxal cavities. Hind femora usually strongly incrassate and toothed. Form broader 15.
14. Elytra more or less parallel-sided. Antennal segments not much larger towards the apex. Eyes without a tract of pubescence along their postero-ventral borders. *Metepisterna* relatively narrow (fig. 25) *Polyoptilus*.
 Elytra markedly contracted towards apex. Antennal segments much larger towards apex. Eyes with a conspicuous tract of pubescence along their postero-ventral borders (fig. 4). *Metepisterna* broader (as fig. 24) *Neodiaphanops*.
15. Head with a pronounced rostrum; postero-ventral borders of eyes with a tract of pubescence as *Neodiaphanops*. Prothorax parallel-sided. Mesosternal process reaching nearly to the level of the posterior borders of the mesocoxal cavities *Diaphanops*.
 Head without such a prominent rostrum, without such tracts of pubescence 16.
16. Prothorax broadest at base, front margin about half as wide as hind margin; prosternal process produced into an acute prominence between the procoxae; side borders of the prothorax at least partially indicated *Carpophagus*.
 Prothorax not broadest at base; prosternal process not produced into a prominence 17.
17. Metasternum raised into a sharp prominence between the middle coxae *Mecynodera*.
 Metasternum not raised into such a prominence 18.
18. Elytra with apical angles produced into a sharp tooth *Ametalla*.
 Apical angles of elytra normal, obtuse; general body form much stouter (fig. 1) *Ametalloides*.
19. Eyes not emarginate, lower surface of body pubescent. Neotropical. *Atalasis*.
 Eyes sharply emarginate; almost entirely glabrous *Sagra*.

Several genera which presumably belong in this group are omitted from the key on account of their absence from the available material. They are

FIG. 1. *Ametalloides punctatus*, general form. 2. *Duboulaia flavipennis*, upper surface of head. 3. *Polyoptilus* sp., upper surface of head. 4. *Neodiaphanops froggatti*, side view of head capsule. 5. *Megamerus kingi*, labium, ventral view. 6. *Zeugophora* (s.str.) *turneri*, upper surface of head. 7. *Z. (Pedrillia) indica*, upper surface of head. 8. *Cucujopsis setifer*, upper surface of head.



Bruchomima Achard (1916), *Macrozeugophora* Achard (1914), *Pedrilliomorpha* Pic (1917), *Plastorsodacne* Brèthes (1928), *Prionesthis* Lacordaire (1845), and *Pseudotoxotus* Blackburn. *Bruchomima* would probably run to *Zeugophora* in my key; it is said to differ in lacking the tooth at the sides of the prothorax. It is represented by a single described species from Madagascar. The Chinese *Macrozeugophora* seems to me a doubtful genus; its describer regarded it as close to both *Zeugophora* and *Pedrillia*, and as these two are now merged it seems that *Macrozeugophora* might fall. *Prionesthis*, founded on a single specimen of an Australian insect seen by Lacordaire and Chapuis but apparently not by any subsequent authors, is said to differ from *Megamerus* chiefly in the non-securiform apical segment of the maxillary palpi. As Lea, in his synopsis of the genus *Megamerus* (Lea 1917), does not regard securiform palpi as a generic character, and actually refers to an unnamed species of the genus which is much smaller than the others and has non-securiform maxillary palpi (hence it might actually prove to be identical with Lacordaire's species), I suspect *Prionesthis funerarius* may belong in the genus *Megamerus*. *Pseudotoxotus* was established by Blackburn (1888) for an Australian species *P. lineatus* Blackburn; the type seems to have remained in Australia and no other student of the group appears to have seen it. However, Mjöberg (1917) described a single specimen of another Australian insect as belonging to this genus, and from his figure of the general habitus and the tarsal structure it is evident that *P. vestitus* Mjöberg is rather closely related to *Polyoptilus* and *Neodiaphanops*—as indeed one might have concluded from Blackburn's description of his insect. But neither author refers to the presence or absence of a pubescent tract along the border of the eyes, so I cannot incorporate *Pseudotoxotus* in my key. Pic's genus is, of course, described in very summary fashion and I am not able to determine whether it is really distinct or whether it could be placed under *Zeugophora* in company with *Pedrillia*. Brèthes proposed the name *Plastorsodacne* for the *Orsodacne grandis* of Blanchard (in Gay, *Historia Física y Política de Chile*); the former author showed that this insect differed in very important characters from *Orsodacne*, and indeed from *Orsodacnini* altogether. He did not consider that *Plastorsodacne* could be retained in the SAGRINAE (in my sense) at all, but placed it in the CROCERINAE, in company with *Psathyrocerus*.

Notes on the Genera.

I. Aulacoscelini.

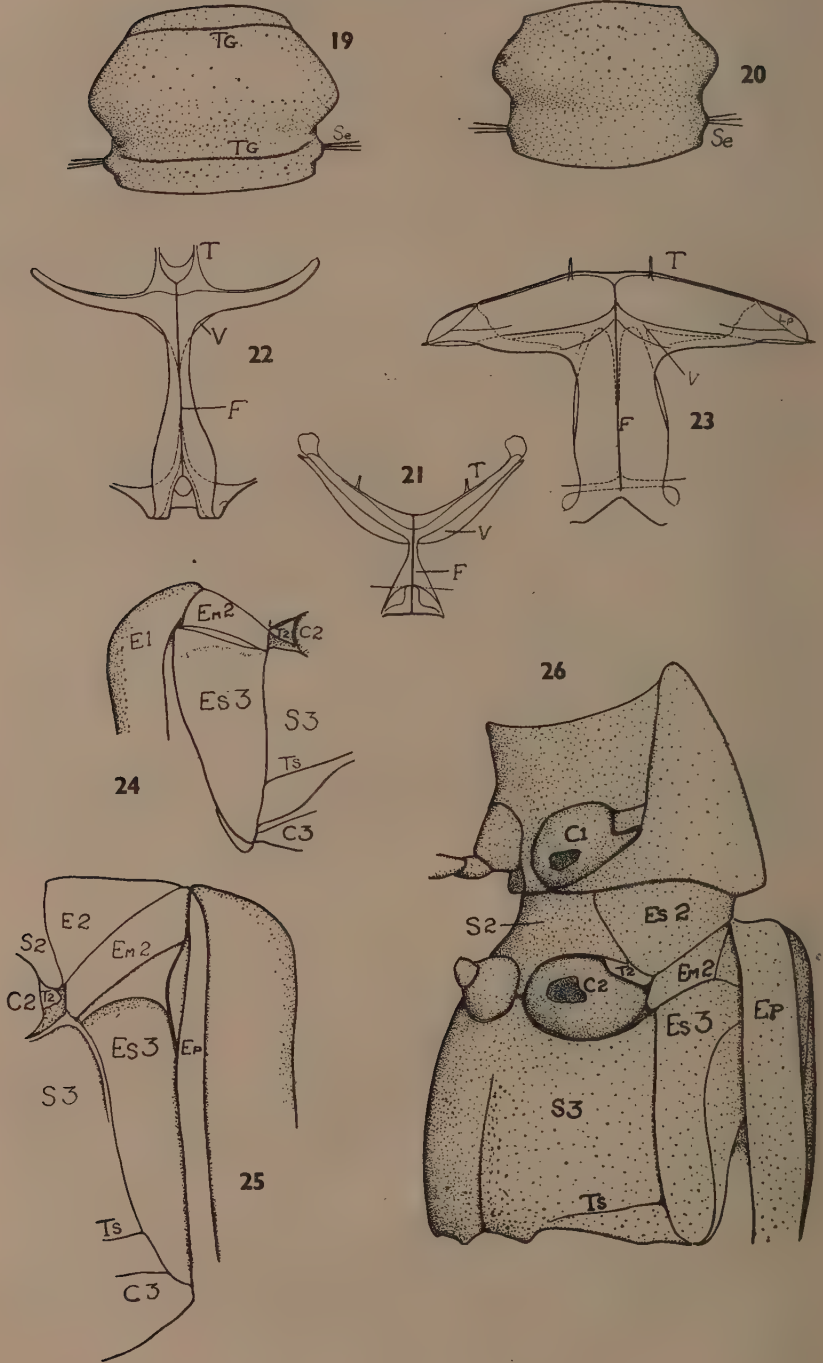
1. *Aulacoscelis* Chevrolat. To assist in settling the relationships of this genus, it may be redefined as follows:—

Form elongate, more or less flattened and parallel-sided.

Integument rather soft, colours not metallic, under surface pubescent.

Head more or less prognathous, eyes not touching front margin of pronotum, clypeus separated from frons by a distinct groove, eyes round, not very prominent. Antennae filiform or slightly serrate, segment 2 at least half as long as 3, inserted at sides of head a little above an imaginary line joining the centre of the eye to the base of the mandible.

Fig. 9. *Hornibius sulcifrons*, wing venation. 10. *Euryope* sp., wing venation. 11. *Atalasis sagroides*, wing venation. 12. *Ametalloides punctatus*, wing venation. 13. *Aulacoscelis hoguei*, wing venation. 14. *Ametalla spinolae*, wing venation. 15. *Cheiloxena insignis*, wing venation. 16. *Neodiaphanops lepturoides*, elytron of ♀. 17. *Mecynoderia coralgica*, hind tarsus. 18. *Polyoptilus* sp., hind tarsus.



Mandibles blunt or somewhat bifid at the apex. Maxillary palpi with last segment largest, more or less ovate but not truncate. Ligula large, semi-membranous, rather deeply bilobed.

Prothorax with sharp and complete lateral margins, prosternum rather narrow between the coxae, the latter transverse, the trochantins small, concealed when the coxae are rotated forward, pronotum with characteristic short longitudinal impressions close to hind margin on each side.

Elytra covering the entire abdomen, confusedly punctured, mesepimeron projecting inward farther than the mesepisternum, behind the outer angle of the coxal cavity.

Metasternum with an almost complete median longitudinal suture, the process in front between the mesocoxae pointed at the apex. Wings with venation of the Chrysomeline type. Hind femora not at all inflated or toothed. Met-endosternite of the Eupodan type.

Abdomen with 5 visible sternites, the first somewhat longer than the remaining ones, its outer anterior angles not prolonged outside the metapleurae, the 5th in the male more or less emarginate at the apex.

Legs: all the tibiae with 2 distinct spurs, the ventral appendage of the 4th tarsal segment rather shallowly bilobed, claws simple.

Aedeagus with the apex of the dorsal process of the tegmen entire ("lateral lobes" of Sharp and Muir absent), tegmen forming a complete ring with a long median ventral projection, median struts absent.

Larvae and habits apparently quite unknown.

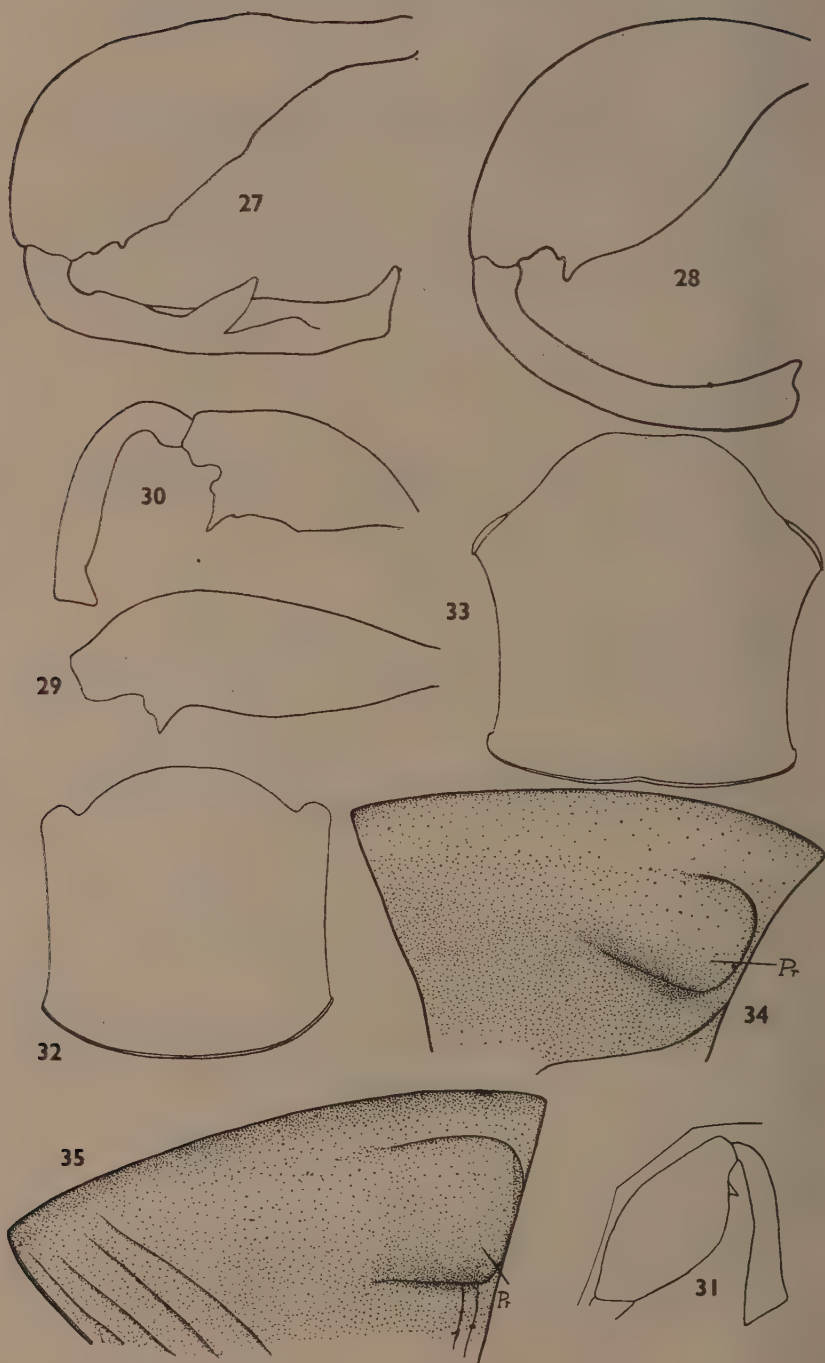
Distribution: Central America from Arizona to Panama, not occurring in the West Indies or Florida.

This genus is one of the most anomalous of the entire family, and from a purely theoretical point of view might even be regarded as meriting a subfamily of its own. It would be very desirable to obtain larvae of some species of *Aulacoscelis*, as the larval habits and structure should be of great assistance in determining its systematic position. If the larva were to prove to have a two- or three-toothed mandible I would consider that it should be removed from the *SAGRINAE* altogether, probably to constitute a separate subfamily.

1. *Aulacoscelis* Chevrolat.—Key to Species.

1. Prothorax strongly contracted in front in the female, distinctly in the male, surface of the pronotum uneven with conspicuous tracts of pubescence; antennae somewhat serrate; head markedly narrowed behind the eyes; elytra flattened on the disc; black, including the scutellum, except for the elytra, which are yellowish (♂) or reddish (♀) . . . *grandis* Jacoby.
- Prothorax not contracted in front, or weakly in the female only, its surface not uneven and without such tracts of pubescence; antennae rarely slightly serrate; head usually not markedly constricted behind the eyes; elytra not so flattened on the disc; coloration different . . . 2.
2. Elytra evidently pubescent throughout . . . 3.
- Elytra glabrous or finely pubescent in part only . . . 6.

Fig. 19. *Zeugophora kwaiensis*, prothorax, dorsal view. 20. *Z. parva*, prothorax, dorsal view. 21. *Psatyrocerus* sp., met-endosternite, postero-dorsal view. 22. *Syneta betulae*, met-endosternite, postero-dorsal view. 23. *Aulacoscelis hogei*, met-endosternite, postero-dorsal view. 24. *Megamerus kingi*, left meso- and meta-pleura, lateral view. 25. *Polyoptilus lacordairei*, left meso- and meta-pleura, lateral view. 26. *Aulacoscelis hogei*, thorax from left-hand side below.



3. Size larger (about 13 mm.); more parallel-sided and elongate; segment 1 of meso-tarsi in male broad, flattened, parallel-sided; prothorax shining, almost impunctate; antennal segments 4 to 11 more than twice as long as wide (female unknown) *elongata* Jacoby.
Size smaller (6-9 mm.); form less elongate; segment 1 of mesotarsi normal in both sexes 4.
4. Elytra, at least in basal half, with conspicuous outstanding pubescence, their surface finely shagreened; pronotum with a few scattered punctures, shining; head and elytra more or less dark-coloured, prothorax at least partly yellowish *melyroides* sp. n.
Elytra without outstanding pubescence, pronotum more closely punctured 5.
5. Smaller (about 6 mm.), prothorax with long conspicuous pubescence at the sides; vertex of head distinctly pubescent with large punctures, coloration dark *fulvipes* Jacoby.
Larger (8-9 mm.), prothorax without such long pubescence, vertex of head less strongly punctured *femorata* Jacoby (*ventralis* Schaeffer.)
6. Sides of prothorax slightly contracted in front, male with segment 1 of mesotarsi as *elongata*; side margins of pronotum rather broadly explanate, its basal margin strongly marked, the disc more flattened than in any species of the genus except *grandis*; elytra very finely shagreened and distinctly punctured, quite dull; body coloration entirely ochreous yellow, tips of femora, tibiae and most of tarsi blackish; head constricted behind the eyes almost as in *grandis* *tibialis* Jacoby.
Pronotum less flattened, its sides not contracted in front, side margins less broadly explanate, basal margin less conspicuous; coloration different 7.
7. Pronotum dull, finely shagreened, with large uniformly scattered punctures; elytra sculptured as in *tibialis*, very finely pubescent at the sides; antennae less than half as long as the body in both sexes, segment 1 of mesotarsi normal in the male *variabilis* Jacoby.
Pronotum shining, not shagreened 8.
8. General form shorter and broader; prothorax conspicuously transverse, sides straight; elytra without raised longitudinal lines, quite dull, each elytron with a tooth on its sutural margin close to the apex *sanguinea* Jacoby.
Form more elongate and parallel-sided; prothorax only very slightly transverse; elytra often with raised longitudinal lines, never toothed on sutural margin 9.
9. Elytra more closely punctured, with 3 distinct longitudinal raised lines *purpurea* Horn.
Elytra very indistinctly punctured 10.
10. Elytra with 3 distinct longitudinal raised lines, the middle one only close to the base (as in *purpurea*), with dull shagreened areas between these lines; mandibles more or less truncate at the apex; segment 1 of mesotarsi in male broadened, more or less as in *tibialis* *candezei* Chapuis.
Elytra with less than 3 longitudinal raised lines, without such dull areas; segment 1 of male mesotarsi normal 11.
11. Mandibles more or less distinctly bifid at the apex; elytra rather dull; with 2 more or less distinct raised lines in the female; general colour yellowish ochreous *hogeii* Jacoby.
Mandibles simple at the apex; elytra shining, with only 1 raised line in the female; reddish *melanocera* Jacoby.

FIG. 27. *Sagra humeralis*, ♂ hind femur and tibia. 28. *S. mouhoti*, ♂ hind femur and tibia.
29. *S. neavei*, ♂ hind femur only. 30. *S. carbunculus*, ♂ hind femur and tibia. 31. *Ametalloides punctatus*, hind femur and tibia. 32. *Sagra stevensi*, pronotum: dorsal view. 33. *S. neavei*, pronotum: dorsal view. 34. *S. jansoni*, pronotum viewed from right side. 35. *S. femorata*, pronotum viewed from right side.

Notes on Species.

1. *Aulacoscelis grandis* Jacoby.

This is represented in the British Museum by 2 specimens, a male and a female: the male being Jacoby's type. The male is 10.5 mm. long, the female 13.5 mm.; in addition to the difference in size, there are several other differences between the sexes, for instance:—In the male the pronotum is only slightly contracted anteriorly and lacks evident depressions, while in the female it is much contracted anteriorly and has large depressions near the front and hind angles; in the male the scutellum is narrower and more pointed, and sparsely clothed with black setae, in the female it is broader and densely clothed with long black setae; the male has the elytra relatively narrower than the female, with a more pronounced longitudinal depression just inside the humeral angles; the antennae in the male have the segments relatively longer and narrower, and largely clothed with white (instead of dark) setae; the last visible abdominal sternite in the male is deeply and rectangularly emarginate in the middle of the apical margin, while in the corresponding place the female has only a small triangular emargination; in the male segment 1 of the middle tarsi is practically parallel-sided for most of its length, while in the female it is regularly narrowed towards the base; the elytra differ in colour in the two sexes. Both specimens are from Ventanas, Durango.

2. *Aulacoscelis elongata* Jacoby.

Represented in the British Museum by a single specimen (the type), which is presumably a male from the broadened basal segment of the mesotarsi and emarginate apex of the last abdominal sternite. It is labelled "Playa Vicente, Mexico", and is 13 mm. long.

3. *Aulacoscelis femorata* Jacoby.

I have included under this species *A. ventralis* Schaeffer (1933), which was stated to differ chiefly in having the 2nd visible abdominal sternite dark. As this character occurs on the type of *femorata* (which Schaeffer had not seen), and the other characters given for *ventralis* do not seem to be of specific value, I am compelled to sink the latter name as a synonym of *femorata*. This species is represented in the British Museum material by 3 males and 9 females, of sizes 7–9.5 mm. and 6.5–9.0 mm. respectively, all from Ventanas, Durango. The males differ from the females in having relatively longer antennae, with the individual segments more flattened, larger heads of a conspicuously squarish shape, the prothorax more transverse with less well-marked hind angles, the surface of the pronotum more closely punctured and finely shagreened in the middle line, the elytra without the well-marked longitudinal ribs of the female, the legs and especially the femora much thicker, the hind margin of the scutellum practically straight (distinctly angled in the female), the second abdominal sternite almost black (ochreous in the female) etc. Two of the females in the British Museum have the elytra of a dark fuscous colour; the smallest male closely resembles *A. melyroides* ♂ in coloration.

4. *Aulacoscelis tibialis* Jacoby.

The British Museum contains the type and one other specimen which seems to belong to this species; the type is a male, while the second specimen—in very poor condition—is a female. The type male is 11 mm. long

and about 5 mm. across the elytra, and the female is of almost exactly the same size; the sexual characters are fairly typical of the genus, the male having the basal segment of the middle tarsi longer, more flattened and parallel-sided than the female, also the last visible abdominal sternite has the hind margin more sharply emarginate in the middle, while the female has a rather pronounced longitudinal ridge on the elytra from the humeral angle. Also most of the antennal segments (especially 3-7) of the male are more flattened than those of the female. The type is labelled "San Juan, Vera Paz".

5. *Aulacoscelis sanguinea* Jacoby.

In the type male of this species the apex of the sutural margin of the elytra is sharply emarginate but does not have a projecting tooth such as is found in the female; the single female specimen from the same locality differs also in having the scutellum rather broader and less acuminate at the apex, the prothorax rather more transverse, and the depressions just inside the humeri of the elytra rather more pronounced. The locality is Chilpancingo, Guerrero. The British Museum also possesses a single specimen bearing the label "S. Mexico" which resembles *sanguinea* but is rather narrower in form, more ochreous in colour, and has the sutural margin of the elytra simple. It probably represents an undescribed species. Length (*A. sanguinea*) ♂ 8.5 mm., ♀ 8.0 mm.

6. *Aulacoscelis melyroides* sp. n.

General form rather elongate and more or less parallel-sided, head and prothorax together a little more than half as long as the elytra; the greatest width across the elytra a little less than half their length. Greatest width of the prothorax about two-thirds of the way to its apex, where it is about two-thirds as wide as the greatest width of the elytra; sides of the prothorax slightly curved, narrowly raised, and sinuate just before the hind angles. Head across the eyes a little narrower than the front margin of the pronotum; antennae at least $\frac{3}{4}$ the length of the body in the ♂, a little more than $\frac{1}{2}$ as long as the body in the female. Head and prothorax shining with a few scattered punctures, more numerous on the head, which has also an evident scattered pubescence. Scutellum very transverse, usually with a few hairs, its apical margin somewhat produced backwards in the middle. Elytra rather dull, finely shagreened, especially in the apical half, with conspicuous outstanding scattered pubescence. Antennae with the third segment about twice as long as the 2nd, the segments from the third to the 7th or 8th becoming gradually longer, 3rd segment in the ♂ with the apex about twice as wide as the base, and its upper (longer) side about twice as long as its apical width; 8th segment with apex about twice as wide as the base, sides $2\frac{1}{2}$ (♀) to $3\frac{1}{2}$ (♂) times as long as its greatest width; 11th segment somewhat pointed at the apex, segments 4 to 10 slightly serrate, all the antennal segments shining but conspicuously pubescent. Tibiae with outstanding pubescence in regular rows. Coloration in the type (♂) slightly bluish-black on the elytra (except the edges), legs (except the bases of the femora and the tarsi), antennae (except the scape) and most of the head and prothorax yellowish testaceous, a large brown cloud in the middle of the pronotum. Basal part of femora, tarsi, antennal scape, and front part of head brownish, under surface chiefly brownish-black except for sides of prothorax and epipleura of elytra, which are yellowish testaceous. In other specimens the dark areas vary to a brownish tint. The female allotype has the prothorax entirely of a bright testaceous yellow, the coloration otherwise resembling that of the male, from which it differs in having the basal half of the elytra more shining and the outstanding pubescence longer and more conspicuous, the scutellum less pubescent, and the antennae shorter.

Length: ♂ 6-7 mm. (5 specimens); ♀ 5-7 mm. (4 specimens).

The type male and allotype female are from MEXICO: Chilpancingo, Guerrero, at 4600 ft. in July; there are 7 more specimens in the British Museum with the same data. They were included under *A. femorata* in the *Biologia Centrali-Americana* material, presumably by Jacoby.

7. *Aulacoscelis fulvipes* Jacoby.

Represented by the type specimen only in the material available; this is about 6 mm. long and seems to be a female; it is labelled "Guanajuato".

8. *Aulacoscelis variabilis* Jacoby.

The sexes seem to differ very little in this species; the British Museum has 14 specimens showing a marked colour dimorphism, 7 being entirely dark fuscous in colour while the other 7 have the prothorax and more or less of the elytral epipleurae reddish-yellow. There is also a dimorphism with respect to the presence of depressions on either side of the middle line of the pronotum; specimens with and without the depressions occur in both the colour forms. The length varies from about 7 to 9 mm. in both colour forms. All the specimens are from Pachuca, Hidalgo, Mexico.

9. *Aulacoscelis purpurea* Horn.

I have not seen a specimen of this insect, and its characterisation in the key rests solely on Horn's description.

10. *Aulacoscelis candezei* Chapuis.

The British Museum contains 1 male and 3 females under this name; it is far from certain that they are conspecific with Chapuis' rather meagrely described species; as the type is presumably in the Paris Museum and not accessible to me the question will have to rest in abeyance. The male is easily distinguished by the widened basal segments of the front and middle tarsi. The species is variable in colour; the single male specimen has the head, prothorax and elytra of a yellowish colour, the antennae, legs and remainder of the body being fuscous; one of the females is similarly coloured but with the yellowish tint slightly darker, another is almost entirely fuscous except for the yellowish edges and suture of the elytra, while the third is intermediate. Chapuis' type seems to have been the dark form. The male specimen is 7.4 mm. long, the females from 7.5 to 8.0 mm. Apparently a North Mexican and mountain form.

11. *Aulacoscelis hogei* Jacoby.

There are 23 specimens of this species in the British Museum; the males differ in having the apex of the last visible abdominal sternite emarginate, and the apices of the mandibles clearly bifid; in the female the latter are blunt or obtusely bilobed and the elytra have more pronounced longitudinal ribs. Length: ♂ 7-9 mm.; ♀ 8-9.5 mm. Many localities, from Durango to Guerrero. (Fig. 26.)

12. *Aulacoscelis melanocera* Stål.

Of this, the type species of the genus, there are 31 specimens in the British Museum and 7 in the Hope Department, Oxford. Differences between the sexes are not very marked, the only reliable one being the emargination of the apical margin of the last visible abdominal sternite in the male. Length:

♂ 6-8 mm.; ♀ 6-8.5 mm. Specimens from South Mexico, Panama and Costa Rica.

II. Hornibiini.

2. *Hornibius* Fairmaire.

The single described species *H. sulcifrons* Fairmaire of the genus occurs in the Tierra del Fuego area; it is evidently a primitive relict comparable with the Cicindelid *Pycnochila* from the same area. At present I am compelled to separate it in a special tribe which is perhaps more closely related to Orsodacnini than to *Aulacoscelis* or Sagrini. The wing venation of *Hornibius* is almost exactly like that of the typical Australian Sagrini (fig. 9), though the head structure shows a considerable resemblance to *Synela*. It would be interesting to investigate the aedeagus and metendosternite of this insect, but unfortunately the available material was too scanty to permit me to do this.

III. Orsodacnini.

3. *Cucujopsis* gen. n.

Size small, form rather flattened and parallel-sided. Head large, prognathous, eyes large, prominent, slightly emarginate in front. Antennae 11-segmented, filiform, rather long, inserted at the sides of the front just before the eyes, segment 2 much shorter than 1 and 3. Clypeus long, labrum short, very transverse, entire. Mandibles outwardly evenly rounded, apices acute. Apical segment of maxillary and labial palpi about as long as the penultimate, slightly thickened in the middle, apex not truncate. Ligula large, membranous, bilobed. Mentum very broad and short, gular sutures obsolete. Prothorax a little narrower at its widest point than the head across the eyes, front margin considerably wider than hind margin, sides in front of the middle bluntly tuberculate. Prosternum of moderate length in front of the coxae, the intercoxal process exceedingly narrow, the coxal cavities closed behind and with a large angular external prolongation exposing the trochantins, the coxae markedly projecting. Legs: all the femora somewhat inflated, particularly those of the hind legs, hind femora with a small tooth below near the apex. All the tibiae straight, with 2 distinct apical spurs. 3rd tarsal segment deeply bilobed, the true 4th segment much shorter than the lobes of the 3rd; claws divergent, not toothed or appendiculate, no evident empodium. Elytra parallel-sided, their total width in repose markedly greater than that of the prothorax, their apical angles somewhat produced, surface confusedly punctured, not striate. Abdominal sternites: 1st nearly as long in the middle line as the next 3 together, with a strong intercoxal process which is strongly bordered at the sides, the 5th sternite nearly as long as the 1st; antero-lateral angles of the first sternite not evidently extending outside the metepisterna.

The genotype is *C. setifer* sp. n.

Cucujopsis setifer sp. n.

Ground colour testaceous, surface clothed with rather long recumbent whitish pubescence, closely punctured. Pronotum with 3 pairs of raised dark brown smooth areas, one pair in front of the middle and nearer to the middle line than to the side margins, a pair situated postero-laterad of these, rather nearer to the side margins than to the middle line and about at the level of the middle of the pronotum, and a third pair situated behind and within these last; similar raised smooth areas occur in more or less regular longitudinal rows on the elytra, becoming larger towards the apex; the first 2 pairs of thoracic raised areas are elongate, the last pair transverse. Long projecting setae are distributed

as follows:—2 on each side at the front angles of the prothorax, one on each of the lateral tubercles, a pair on the hind angles of the prothorax, and 2 more or less regular rows on each elytron, one starting from just inside the humeral angle, and another midway between this and the suture, each row with about 4 setae. In addition, shorter projecting setae occur laterally on the elytra, on the tibiae, and elsewhere. Antennae about $\frac{3}{4}$ as long as the entire insect, entirely testaceous, all the segments elongate, 1st about twice as long as



FIG. 36.—*Cucujopsis* gen. n. *setifer* sp. n. Type.

wide, 2nd a little less than twice as long as wide and about $\frac{1}{2}$ as long as the 1st, 3rd about as long as the first, segments 3 to 11 of similar shape but very slightly increasing in size, each with the apex about twice as wide as the base and 3 or 4 times as long as the apical width. Legs entirely testaceous, hind femora with a small blunt postero-ventral tooth, about one-fifth from the apex, all the femora slightly darkened in the apical half. Length 3.9 mm., width 1.27 mm.

This remarkable species is represented by a single excellent specimen (the type) from N. QUEENSLAND: Kuranda (*R. E. Turner*), in 1913. It is a small insect of a light brownish colour, with something of the appearance of a small Cucujid, and differs extremely from the typical Australian Sagrini. The resemblance to CUCUJIDAE which suggested the name is in my view not without significance, as CHRYSOMELIDAE are generally regarded as closely related to CERAMBYCIDAE, in which family the primitive *Parandra* has a Cucujoid facies, and I have published elsewhere my reasons for supposing that both families had a common origin from Cucujoid ancestors. The nearest existing relatives of *Cucujopsis* would appear to be *Orsodacne* and *Hornibius*, the first of these genera being perhaps rather more closely related to it. I have not investigated the wings of *Cucujopsis*; in view of the small size of the insect the venation would probably prove to be somewhat reduced.

4. *Orsodacne* Latreille.

The species of the genus, with one or two doubtful exceptions, are holarctic in distribution. Three were described, far back in the last century, from Chile; it is interesting that the only one of these which appears to have been studied by any author since its description has been shown not to be an *Orsodacne* and only very doubtfully a member of the present group at all. The other exception is *O. splendida* described by Montrouzier in 1857 from Woodlark Island (New Guinea); this is very far from the occurrence of any other known *Orsodacne* but suggestively near the locality of *Cucujopsis* (North Queensland). Setting these aside, the genus appears to comprise a single North American species, two from most of Europe, and one from Persia. These may be distinguished as follows:—

1. Upper surface distinctly pubescent throughout 2.
 Pubescence of pronotum and elytra very short or absent 3.
2. Whole upper surface more closely punctured and pubescent; scutellum distinctly and rather closely punctured; colour testaceous to blackish.
 Europe *lineola* Panz.
 Pubescence and punctuation of upper surface much more scattered; scutellum almost impunctate. Persia *variabilis* Baly.
3. Pronotum duller, surface slightly uneven, finely shagreened; each puncture usually with a short but distinct seta. N. America *atra* Ahr.
 Pronotum more shining, surface smooth between the punctures, latter without evident setae. Europe *cerasi* L.

5. *Syneta* Lacordaire.

The inclusion of this genus in the *SAGRINAE* may seem scarcely justified when one lists the characters in which it differs from the rest of the subfamily. Among them may be mentioned the ligula, which is only very feebly bifid, the open front coxal cavities, the aedeagus, the met-endosternite (fig. 22), and the reduced wing venation. In fact, it can scarcely be denied that *Syneta* in the adult state at least differs from the type of the *SAGRINAE* in more, and more important, characters than do the *DONACIINAE* or the *BRUCHIDAE*. Why then, it may be asked, include the genus here? The chief reason is its evident connection with *Orsodacne*, which genus is unquestionably a member of the group as I have defined it; it is also to be noted that if *Syneta* is excluded from the *SAGRINAE* there is no other group in the family with which it could be placed, and that the characters in which *Syneta* differs from the other *SAGRINAE* all appear to be specialised. So I think it is possible to keep *Syneta* in the group as an aberrant type. Unfortunately, although a species of the genus is recorded as a pest of fruit trees in western North America, there appear to be no details of its larval structure published. The genus *Tricolema*, erected by Crotch for a Californian species *T. anomala* Crotch, bears a relation to *Syneta* s.str. rather similar to that of *Syneta* to the *Orsodacnini*; I regard it as a subgenus only, distinguished as follows from *Syneta* s.str.:—

Tibial spurs absent on all tibiae; male with abdominal sternites 2–4 sharply narrowed in the middle and the 5th unusually large; female with simple tarsal claws; elytra quite confusedly punctured, with epipleurae very weak; whole body clothed with long recumbent pubescence; Californian

Tricolema Crotch.

- 1 or 2 tibial spurs present on all the tibiae; abdominal sternites of the male normal; tarsal claws bifid in both sexes; punctures of elytra tending to form rows; epipleurae distinct; pubescence of body shorter, not fully recumbent; holarctic *Syneta* s.str.

The species of *Syneta* are duller looking and more strongly sculptured than those of *Orsodacne*; the adults appear always to occur on trees, chiefly *Betula* and *Salicaceae*. A number of species occur in the China-Japan area, chiefly described by Gressitt (1942), one occurs (on *Betula*) in northern Europe, another (also apparently on *Betula*) in eastern North America, and several in western North America. The larva of *S. albida* Leconte, the "Western Fruit Beetle", is said to live in the roots of trees.

6. *Zeugophora* Kunze (including *Pedrillia* Westwood).

The insects included in this genus are normally smaller and of broader form than *Orsodacne* and *Syneta*; like those two genera, *Zeugophora* has species throughout the Holarctic region, but in addition there are numerous species in the Ethiopian and Oriental regions; these were formerly placed in a separate genus *Pedrillia* which was usually put in the MEGALOPODINAE. In my view (see also Bryant 1943) these non-holarctic species are not more than subgenerically distinct from the holarctic ones, so I am treating *Pedrillia* as a subgenus. The following key includes all the species which have been available to me, and two Japanese ones which were exceptionally well described and figured by Chujo (1932). Four more Formosan species are well described and figured by Chujo (1937).

1. Eyes less strongly emarginate (fig. 5); frons with an impressed line between the eyes, posterior to the fronto-clypeal suture; the basal angles of the prothorax simple, without laterally projecting setae. Holarctic (excluding Japan) *Zeugophora* s.str. 2.
- Eyes more strongly emarginate (fig. 6); frons without a transverse impressed line posterior to the fronto-clypeal suture; basal angles of the prothorax more or less tuberculate, bearing about three laterally projecting setae. Oriental (including Japan) and Ethiopian (including Madagascar) subgenus *Pedrillia* Westwood 9.
2. Front angles of the prothorax more prominent, somewhat projecting; upper surface entirely testaceous 3.
- Front angles of prothorax less prominent; upper surface not wholly testaceous 4.
3. Insect entirely testaceous; head with a wide smooth median line above; punctuation of elytra very coarse, tending to lines near the suture. Eastern North America. Length 3.5 mm. (type) *kirbyi* Baly.
- Meso- and metasterna and abdomen black; head without such a distinct median smooth line; elytral punctuation less coarse, not at all lineate. Northern Europe. Length 3.5 to 4 mm. *turneri* Power.
4. Vertex of head at least at the sides densely and coarsely punctured. North American 5.
- Vertex of head not densely punctured. Chiefly European 7.
5. Head and prothorax entirely yellowish; elytra yellowish with a broad common sutural black band nearly reaching the apex; pubescence on head and elytra very conspicuous and outstanding; size larger (3.5-4 mm.). Oregon and N. California *californica* Crotch.
- Basal part of head usually black, prothorax usually with dark marks; pubescence less conspicuous; size smaller (3-3.5 mm.) 6.

6. Elytra much more finely punctured; black, front of head, prothorax, legs, and base of antennae yellowish *consanguinea* Crotch.
Elytra more coarsely punctured, prothorax with dark patches on each side of the disc, leaving a yellowish middle line; elytra usually blackish with a large common yellowish discal spot *varians* Crotch.
7. Lateral tubercles of prothorax sharp at the apex; base of head black; legs, prothorax, front of head, yellowish, rest of body blackish. Length 3 mm. Europe *flavicollis* Marshall.
Lateral tubercles of prothorax blunt; head entirely yellow 8.
8. Scutellum black; segment 4 of antennae dark like 5; size small (3 mm.). Black, head, prothorax, legs, antennal segments 1-3 yellowish. Europe *subspinosa* Fabricius.
Scutellum yellow; segment 4 of antennae pale like 3; size larger (4 mm.). Europe, N. America *scutellaris* Suffrian.
9. Pronotum with distinct transverse impressed lines close to the apical and basal margins. Africa, Madagascar 19.
Pronotum without transverse impressed lines; Oriental and Japanese 10.
10. Head and prothorax entirely testaceous; pronotum diffusely punctured, the punctures not larger than the facets of the compound eye 11.
Head and prothorax black, or pronotum closely to densely punctured with punctures larger than the facets of the compound eyes 14.
11. Sides of the prothorax behind the tubercles longer, almost half as long as the prothorax, slightly diverging posteriorly. Colour variable. Length 3.3-4 mm. Ceylon *murrayi* Clark.
Sides of prothorax behind the tubercles shorter, converging posteriorly 12.
12. Prothorax with lateral tubercles less prominent, their hind edges making an angle of about 45 degrees with the longitudinal axis of the body; legs mainly black. Length about 4 mm. Indian *longicornis* Westwood.
Prothorax with the lateral tubercles more prominent, their hind edges making an angle of about 60 degrees with the longitudinal axis of the body; legs mainly yellow 13.
13. Antennae mainly black, segment 3 twice as long as 2; size smaller (4 mm.). Indian *indica* Jacoby.
Antennae fulvous, basal segments darker, segment 3 one and a half times as long as 2; size larger (6 mm.). Formosan *ruficollis* Chujo.
14. Entirely testaceous, except base of head black; pronotum fairly closely punctured; size smaller (3 mm.). Northern India *parva* sp. n.
Otherwise coloured; size larger (4 mm. or more); Japan 15.
15. Prothorax narrower, the lateral tubercles less projecting (fig. 20), very coarsely but not quite densely punctured *varipes* Jacoby.
Prothorax broader, the lateral tubercles more projecting (as in fig. 19); less coarsely punctured 16.
16. Pronotum with a distinct impression across the base, closely and moderately strongly punctured; elytra testaceous with a ring-shaped dark mark towards the apex of each *annulata* Baly.
Pronotum without a transverse impression, either densely or diffusely punctured; elytra otherwise marked 17.
17. Prothorax dull, very densely punctured, the basal tubercles exceptionally prominent *unifasciata* Jacoby.
Prothorax shining, diffusely to closely punctured, the basal tubercles less prominent 18.
18. Prothorax closely punctured, with a slight median longitudinal impression; undersurface not entirely black *nigricollis* Jacoby.
Prothorax diffusely punctured; underside and legs entirely black *nitida* Chujo.
19. Head and prothorax and elytra entirely testaceous; vertex very diffusely punctured throughout; antennae of two sharply separated colours 20.

- One or other of these parts partly or wholly black; antennae not sharply bicoloured 23.
20. Legs and undersurface entirely testaceous; antennal segments 5-11 piceous, 4 more or less infusate, 1-3 testaceous. S. African *testaceipes* Pic. 21.
- Legs not entirely testaceous 21.
21. Tarsi and apices of middle and hind tibiae only black; segments 1-4 of antennae testaceous, 5-11 black. Madagascar *madagascariensis* Jacoby. Middle and hind tibiae largely black 22.
22. Middle and hind tibiae pale at the base; antennal segment 4 mainly testaceous. South African *africana* Bryant. Middle and hind tibiae entirely black; segment 4 of antennae mainly piceous. East African *kwaiensis* Weise.
23. Elytra blue-black, rest of body testaceous; antennae blackish, basal segments partly yellow, tarsi, middle and hind tibiae, and outer edge of front tibiae, black. E. Africa *bicolor* Achard. Elytra not entirely blue-black 24.
24. Size larger (4-5 mm.); antennae entirely testaceous except tip of the last segment; head black behind the antennal insertions with very sparse punctuation; elytra with basal margin and humeri, also scutellum, black; legs mainly testaceous with dark bands along the femora. East Africa *humeralis* Achard. Size smaller (about 3 mm.); basal border of elytra and base of head not entirely black. South Africa 25.
25. Vertex of head with normal diffuse punctuation *capensis* Bryant. Vertex of head very strongly punctured, densely at the sides towards the eyes *variabilis* Achard.

As far as known, the species of *Zeugophora* s.str. seem to be attached to Salicaceous trees, chiefly species of *Populus*, the larvae having leaf-mining habits. Böving and Craighead (1931) figure the larva of *Z. scutellaris* Suffrian. Nothing seems to be recorded concerning the habits of the species of the subgenus *Pedrillia*, except for one record of *Z. andrewsi* on sandalwood in Madras (Chatterjee & Bhasin 1936); most of them occur in more or less tropical regions where Salicaceous plants are not found.

Zeugophora (Pedrillia) parva sp. n.

With the general characters of *Zeugophora* and of the subgenus *Pedrillia*. Head: eyes, seen from above, separated by not quite twice their apparent width, the vertex between them punctured moderately closely with punctures about as large as the facets of the compound eyes, except along the smooth median line. Segment 1 of antennae almost as long as the apparent width of the eye, slightly curved, apically nearly one-third as wide as its length, segment 2 of similar width but barely two-thirds as long, segments 3-4 as long as 1 but more slender, segments 5-11 becoming very gradually shorter, all about as wide as 1, segment 11 about three times as wide as long. Thorax: pronotum of the characteristic shape of the genus, without transverse or longitudinal impressed lines (fig. 20), the hind margin slightly wider than the front margin, its surface closely punctured with rather large punctures, the latter slightly larger than the facets of the compound eyes. Elytra slightly widened to just behind the middle, their surface closely to densely covered with punctures rather larger than those of the pronotum. Colour: entirely testaceous except for the more or less fuscous apex of the antennae and the base of the head, which is black with the black colour extending forward on each side along the inner margins of the eyes as far as the antennal insertions. Size: body length 3-3.2 mm., width across the prothorax 0.9 mm.

Two specimens, including the type, in the British Museum, presented by Prof. H. G. Champion, and bearing the label "S. Garwhal, Kumaon, 6,500 ft."

7. *Hemydacne* Jacoby.

It is very doubtful whether this genus belongs in the *SAGRINAE* at all; I have not been able to verify the presence of a bilobed ligula in the scanty material available, and the head and prothorax of *Hemydacne* differ very much from those of others of this group. Other possible positions for it are in the *EUMOLPINAE* or *CRIOCERINAE*.

IV. *Sagrini*.

8. *Duboulaia* Baly.

There are three West Australian species described under this generic name; two of them would run to this genus in my key, but the third would probably be traced to *Ametalloides*, from which genus it differs in the very much less prominent eyes and in the presence of a raised flange along the postero-ventral borders of the eyes, also in the shape of the prothorax. The logical course would probably be to erect a new genus for this species, *Duboulaia rugosa* Baly.

9. *Coolgardica* Blackburn.

Evidently related to the last, this genus has so far only one described West Australian species; this is distinctly atypical among the *Sagrini* in its shape, which is suggestive of *Orsodacne* or even of the Longicorn *Spondylus*.

10. *Megamerus* Macleay.

Lea (1917) gives a key to distinguish 4 species of *Megamerus*, 3 of which are represented in the material available to me; he also mentions 2 more undescribed ones. There has evidently been some confusion over the species of this genus. The original type of *M. kingii* does not appear to have been seen by later authors, with the result that any species of the genus has been more or less uncritically labelled *M. kingii* Macleay in collections. Boisduval had a species of the genus which he described as *M. prionesthis* in 1835, but later sank as a synonym of *kingii*. Lacordaire (1845) accepted *prionesthis* as a synonym of *kingii*, while adopting the name *Prionesthis* for a new genus which he regarded as being closely related to *Megamerus*. The British Museum contains a specimen from Baly's collection with the note "This specimen is the one described by Boisduval," and which, according to Lea's key, is a male of *M. mandibularis* Blackburn. Also, by the description, *Prionesthis funerarius* Lacordaire seems to agree rather well with one of the undescribed species of *Megamerus* mentioned by Lea. One may thus conclude that very probably *Megamerus mandibularis* Blackburn (1892) = *M. kingii* Boisduval (1835) = *M. prionesthis* Boisduval (1835), and possibly the genus *Prionesthis* Lacordaire (1845) = *Megamerus* Macleay (1827).

11. *Polyoptilus* Germar.

This genus is one of the most difficult of the *Sagrini* to define; the species are often very Longicorn-like in general appearance and several of them show a pronounced sexual dimorphism and considerable variability in size and colour. Of the ten species hitherto described under *Polyoptilus*, *P. pachytoides* Baly is in my view better placed in the genus *Neodiaphanops* Blackburn,

while the types of *P. waterhousei* Baly and *P. robustus* Blackburn do not seem to be specifically distinct from *P. lacordairei*, but there are two specimens in the British Museum which appear to belong to an undescribed species of the genus, and one or two others might also represent undescribed species. To assist in the study of this difficult genus I am giving a tentative key to distinguish the species known to me:—

1. General body form stouter; entirely black; head and prothorax above closely punctured, glabrous; elytra with more or less regular rows of punctures and with punctures on the interstices; hind femora distinctly angled in the middle below with a small subapical tooth; lower surface with very short and inconspicuous pubescence. *P. torridus* Blackburn.
General body form less stout; not entirely black; lower surface with longer pubescence 2.
2. Hind femora slender, without a subapical tooth below; head and prothorax pubescent above in the male 3.
Hind femora with a small subapical tooth, head and prothorax not pubescent above 4.
3. Antennae fulvous or light brown *P. decolor* Newman.
Antennae black or fuscous *P. gracilis* Blackburn.
4. Elytra with 4 distinct raised longitudinal lines *P. costatus* Blackburn.
Elytra without or with more than 4 raised longitudinal lines 5.
5. Pronotum dull, brown, strongly punctured *P. asper* sp. n.
Pronotum fuscous, shining, finely punctured 6.
6. Elytra unicolorous dark brownish, shining *P. pascoei* Baly.
Elytra at least in part fulvous, not unicolorous
P. lacordairei Germ. (*robustus* Blackburn, *waterhousei* Baly; female = *erichsoni* German).

Of *P. torridus* two specimens, including the type, are available; from the short antennae and reduced wings they would appear to be females. There are 12 males of *decolor* in the British Museum and 8 in the Hope Department: 2 specimens labelled "*decolor* female sec Baly" are in the British Museum; they are shorter and broader than the males, without evident pubescence on the head and pronotum, the antennae are brownish and about half as long as the body ($\frac{3}{8}$ as long in the males), the elytra bright fulvous with rather irregular brownish markings, short and not closely fitting together so that the apex of the abdomen is uncovered; wings appear to be absent. *P. gracilis* is represented by 7 specimens (probably all males) in the British Museum. In the same collection are 4 specimens of *P. costatus*, without obvious sexual differences.

Polyoptilus asper sp. n.

Elongate, rather parallel-sided, prevailing colour brown, dull. Prothorax about as long as its greatest width, the latter being about two-thirds of the way from the base to the apex, sides sinuate behind the middle, curving on to the front margin in front so that the front angles are obsolete. Base of the head about two-thirds as wide as the base of the prothorax, the eyes projecting prominently, the maximum width across them being fully equal to the maximum width of the prothorax and almost twice the width of the base of the head. Antennae almost as long as the entire body (male?), segment 1 somewhat inflated, about $1\frac{1}{2}$ times as long as its greatest width, segment 2 not quite as long as wide and about two-fifths as long as 1, segment 3 rather longer than wide and twice as long as 2, segment 4 longer than 2 and 3 together, its apex about twice as wide as its base, about $2\frac{1}{2}$ times as long as its apical width, segments 5 to 9 similar but progressively longer,

10 and 11 about as long as 9, the 11th narrower than the others at the base and somewhat pointed at the apex. Maximum width of the elytra, just behind the humeral angles, about one and two-thirds times the maximum width of the prothorax, elytra slightly contracted immediately behind this then almost parallel-sided till close to the apex, where they are separately rounded, with obtuse apical angles; length of the elytra about $2\frac{1}{2}$ times the maximum width across them. Femora somewhat thickened, especially hind femora, the latter markedly angled in the middle below, with a distinct subapical tooth.

Head and pronotum of a somewhat darker brown than the rest of the body, elytra rather lighter, more or less fulvous. Head very densely and evenly punctured, quite dull; punctures of the pronotum a little larger than those of the head, rather irregularly distributed, tending to be sparser near the middle line and becoming dense in parts at the sides, the pronotum thus appearing to be somewhat shining on the central part; elytra with punctures on an average somewhat larger than those of the pronotum, arranged in irregular longitudinal lines, the interstices between the lines on an average about as wide as the punctures and slightly raised in parts, the apical fifth of the elytra with quite irregular punctuation, the sutural stria deep and complete, the elytra appearing somewhat shining; scutellum smooth, about as wide as long, its hind margin rounded. Legs unicolorous, the tibiae somewhat sinuate, especially on the front legs. Length 9.5–11.5 mm.

Two specimens in the British Museum, both from the Jacoby collection and labelled only "Australia".

P. pascoei is represented in the British Museum material solely by the type which is probably a male. *P. lacordairei* is evidently a variable species; there are 22 males and 12 females in the British Museum (including the types of *robustus* and *waterhousei*) and 5 males and 3 females from the Hope Department in the material at my disposal. The female of this species is considerably different from the male and was at first regarded as a separate species (*erichsoni* Germar). *P. irregularis* Lea I have not seen; to judge from the description the type specimen is a male, which in sculpture seems to agree fairly closely with *P. torridus*. However, the latter species is described from the Cape York area, so that it is in any case unlikely to be conspecific with *irregularis* which is described from New South Wales. The species of *Polyoptilus* have been too little collected for any useful conclusions to be based on their distribution.

12. *Neodiaphanops* Blackburn.

This genus was originally founded on the single species *N. froggatti* Blackburn; *Polyoptilus pachytoides* Baly seems to me to be congeneric with Blackburn's species and I am referring a new species described below to the same genus—as a result the genus needs to be redefined as follows:—

Head fairly long with rather small finely faceted eyes, which are oval and very slightly emarginate in the upper part of the front margin; a distinct tract of pubescence occurs along the postero-ventral edge of each eye but the head capsule is not flanged in this area. Antennae not longer than the body in the male, conspicuously thickened towards the apex. Maxillary palpi with the last segment oval or slightly truncate, not securiform, about twice as long as the penultimate segment. Prothorax more or less cylindrical, usually slightly constricted just in front of the base, sides not markedly protuberant just behind front angles; prosternal process narrow, rather suddenly deflexed but not angled between the coxae, its apex rounded. Mesosternal intercoxal process broader than the prosternal one, not reaching as far back as hind borders of the coxal cavities. Metepisterna rather broad, triangular, the front margin at least half as long as the inner margin. The first visible abdominal sternite not quite as long as the remaining four

together. Meta-femora not very much thickened, their lower edge more or less angled about two-thirds of the way to the apex, between this and the apex with a small sharp tooth posteriorly. 4th tarsal segment almost as long as the lobes of the third, these latter about as long as the basal part of the 3rd segment. Elytra tapering towards the apex, somewhat flattened, not at all striate. Upper surface of the head always more or less pubescent, pronotum and usually also elytra with at least traces of pubescence.

The species at present known may be distinguished as follows :—

1. Eyes more prominent, elytra glabrous, fully developed, reddish-ochreous with a black sutural stripe and another extending from near the humerus almost to the apex. North Australia *pachytoides* Baly.
Eyes less prominent; elytra more or less pubescent 2.
2. Elytra slightly divergent posteriorly ♂♀, pubescent along suture and towards apex only, elytra ochreous with a large irregular elongate dark patch in the middle, suture black, also outer edges. ♂ and ♀ not very different. N.W. Australia *froggatti* Blackburn.
Elytra completely coadapted ♂, divergent and not reaching apex of abdomen ♀, with numerous longitudinal bands of conspicuous white pubescence in ♂, with a patch of pubescence inside the humerus ♀, elytra in ♀ with ground colour more reddish, without such a dark patch midway between the suture and the outer margin *lepturoides* sp. n.

. *Neodiaphanops lepturoides* sp. n.

Male : General shape similar to male of *N. froggatti* or *N. pachytoides* but a little narrower. Head rather longer than the prothorax, the latter about as wide as long and less than a third as long as the elytra; the latter are more than $1\frac{1}{2}$ times as broad as the prothorax at their base and tapered towards the apex, the apical angles being rounded. Legs rather long and slender, antennae distinctly thickened towards the apex and about $\frac{2}{3}$ as long as the body. Fully winged. Surface of the body and legs largely covered with dense white recumbent pubescence, which is also present on the elytra as follows : a broad band along the suture, one along the outer margin, and 4 more between these, the first and third of these from the suture incomplete at the base, all of them becoming confluent at the apex, the interspaces generally narrower than the bands of pubescence. General body colour brownish-black, slightly shining, head and prothorax closely punctured, elytra more shining, with extensive reddish-yellow markings, the dark colour forming a broad sutural band, a humeral patch, an interrupted marginal band, and an incomplete band just inside the marginal one. Antennae brownish, finely and closely pubescent, the segments from the 2nd onwards becoming progressively longer and up to the 8th progressively thicker, slightly serrate. Prothorax almost parallel-sided, with a feeble transverse impression right across just in front of the base and a rather stronger one just behind the front margin, scutellum thickly clothed with white pubescence. Elytra with an incomplete curved longitudinal impression starting just inside the humeral protuberance. Lower margin of hind femora slightly angled about one-third from the apex, with a small sharp tooth on the postero-ventral side very close to the apex.

Female : Much stouter than the male, elytra shorter, not fully covering the abdomen, their sutural margins not fitting together posteriorly, wings reduced. Pubescence of whole body shorter and less conspicuously white than in the male, the pubescent bands absent from the elytra except the sutural one, which is weak, and a patch just within the humeral angle. Prothorax distinctly transverse; antennae only about $\frac{1}{2}$ as long as the body. General body colour and elytral pattern as in the male.

Size : ♂ 9 mm. long, width across humeri 3.2 mm.; ♀ 11–14 mm. long, width across humeri 4.5–5.5 mm.

1 male (the type) and 2 females from CENTRAL AUSTRALIA : Hermannsburg (H. J. Hillier), 1911.

Neodiaphanops has been regarded as most closely related to *Diaphanops* and *Carpophagus*, but in my view it is more closely allied to *Polyoptilus* than to either of these.

13. *Rhagiosoma* Chapuis.

This is of interest as being the only typical *Sagrini* genus occurring outside Australia (*Sagra* itself must be regarded as a distinctly atypical genus, and *Atalasis* is evidently related to *Sagra*). It has obvious resemblances to *Megamerus* but also has some similarity to the more specialised genus *Mecynoderus*. There are 5 species described, of which specimens of 2 have been available to me for study. Sexual differences do not seem very obvious in this genus, although *R. madagascariense* shows considerable variation in size and colour. Pic (1914) described *R. obscurithorax* with the brief locality "East Africa"; if this is correct, his species is the only *Rhagiosoma* known from outside Madagascar.

14. *Diaphanops* Schonherr.

According to Lea (1918) there is only one known species of this genus, *D. westermanni* Boheman, Blackburn's species *D. meyricki* and *D. parallelus* being nothing more than varieties of this very variable species. I have not been able to find any secondary sexual characters in this insect.

15. *Carpophagus* Macleay.

Much emphasis has been placed on the resemblance of this genus to BRUCHIDÆ, but I do not think that *Carpophagus* is in any way directly related to that family. The published data on the habits of *C. banksiae* mention it as occurring on the foliage of the Proteaceous genus *Banksia* and also on Cycads (*Macrozamia*). If the latter plant is really the food plant of the insect, it would be a very interesting fact, suggesting the possibility that the Chrysomelids may be an older group than I have supposed and primitively attached to Cycadophyta but having almost exclusively adapted themselves to Angiospermae when the latter appeared. There are two described species, both represented in the British Museum. In both of them the males may be distinguished by having the middle of the apical margin of the last visible abdominal sternite depressed in the middle; in *C. banksiae* the males have the elytra more or less bright reddish, while in the female they are dark brown. Of *C. banksiae* I have seen 12 ♂ and 5 ♀ in the British Museum and 6 ♂ and 4 ♀ from the Hope Department; the lengths are ♂ 16–21 mm., ♀ 19–22 mm. *C. excavatus* Baly is represented by 1 ♂ and 4 ♀ (including the type) in the British Museum. The male is 16 mm. long and the females 18–21 mm. The two species may be distinguished as follows :—

Prothorax at its base slightly wider than its length in the middle line. Elytra very distinctly rounded at the sides, with uniformly distributed pubescence, reddish in ♂, dark brown in ♀. Hind femora strongly inflated. Upper surface of head with scattered pubescence	<i>banksiae</i> Boisduval.
Prothorax slightly longer in middle line than its basal width. Elytra hardly rounded at the sides, with numerous small patches of dense white pubescence, between them dark fuscous, glabrous and shining in both sexes. Hind femora much less inflated. Upper surface of head with close whitish pubescence and a bare dark area along the middle line . . .	<i>excavatus</i> Baly.

16. *Mecynodera* Hope.

It is evident that this is one of the more specialised genera of the Australian Sagrini; the wing-venation departs from the typical form, having the anal veins reduced and modified, approaching the condition in *Ametalla*. *Mecynodera* has some resemblance to *Rhagiosoma*, and has 3 species at present described—specimens of all of them, and the types of two, have been available to me in the British Museum. *M. coxalgica* Boisduval is evidently an abundant species of which plentiful material is available; the main collection at the British Museum has 25 ♂ and 22 ♀, and the material lent me by the Hope Department contains 10 ♂ and 18 ♀. Considerable variability is shown in size and colour pattern; the type form has a characteristic pattern of red marks on a black ground, but in some specimens the red markings are reduced to comparatively small spots, and in others the elytra are entirely reddish with obscure darker marks. The males vary from 8.5 to 15.5 mm. in length, and the females from 10 to 17.5 mm. *M. balyi* Clark has 4 ♂ and 4 ♀ in the British Museum (the type is a ♂), and a single ♂ in the Hope Department; the males are from 9.5 to 11 mm. long and the females from 10.5 to 11 mm. The unique type of *M. wickhami* Waterhouse is a male in the British Museum; it is 13.5 mm. long. The three species may be roughly distinguished as follows:—

1. Prothorax rather dull, at least in part closely and rather rugosely punctured. Elytra very distinctly punctured, the punctures in irregular longitudinal lines *coxalgica* Boisduval.
Prothorax shining, the punctuation scattered or obsolete. Punctuation of elytra obsolete 2.
2. Elytra with a well-marked slightly curved impressed line just inside the humeral protuberances, with a red and black pattern resembling that of *coxalgica* *balyi* Clark.
Elytra with the depression inside the humeral protuberance short and much less marked, the basal third and the apical third black, the middle third red, the two colours separated by almost straight lines *wickhami* Waterhouse.

The males of *Mecynodera* have longer antennae than the females; they have the first visible abdominal sternite more or less depressed in the middle and with close pubescence in the depression, and the 5th visible sternite more or less distinctly depressed in the middle of its apical margin. The latter character is most strongly marked in *coxalgica* and very weak in *wickhami*, while the converse is true of the second character mentioned.

17. *Ametalloides* gen. n.

Antennae not more than half as long as the body, simple. Eyes slightly emarginate in front, their long (dorso-ventral) axis about twice as long as their width. Head with rostrum not very strongly developed, the distance from midway between the bases of the antennae to the base of the labrum slightly greater than the width of the clypeus; labrum very slightly emarginate in front; the crossed frontal grooves present but not very deep. Ligula semi-coriaceous, fairly deeply bilobed; maxillary and labial palpi rather short, the last segment of the maxillary palpi largest and ovate. Head without a raised flange or tract of pubescence along the postero-ventral border of the eyes. Prothorax transverse, broadest in front, the front angles not produced into tubercles, side margins absent. Front coxae not projecting, their trochantins exposed, the inter-coxal process of the prosternum bent down rather abruptly between the coxae and truncate at its apex, not projecting behind the post-coxal process of the propleuron. Mesosternum

simple, the inter-coxal process not quite reaching the level of the hind margins of the coxal cavities. Metepisterna not very strongly broadened in front; the longitudinal suture of the metasternum complete. All the tibiae without visible spurs, the hind femora inflated, their lower edge rather sharp but not angled in the middle, with a sharp tooth just behind this edge close to the apex (fig. 31). Tarsi with segment 3 deeply bilobed, the lobes much longer than the basal part of the segment, the 4th segment less than half as long as the lobes of the 3rd, claws simple. 1st visible abdominal sternite about as long in the middle line as the remaining 4 combined. Elytra with a deep sutural stria in the posterior $\frac{2}{3}$, their apical angles not produced into a tooth.

The genotype is *A. punctatus* sp. n.

Ametalloides punctatus sp. n.

General colour more or less fuscous, elytra mainly testaceous brownish with scattered longitudinal dark marks. Lower surface, legs, front of head, scutellum evidently though not very closely covered with fulvous pubescence, pronotum and elytra with very short and inconspicuous setae in the large punctures. General body surface closely punctured, dull, with large punctures densely covering most of the pronotum and in very irregular rows on the elytra. Pronotum with a somewhat smoother area along the front margin and on either side of the middle line, very slightly depressed in the middle line just before the base. Head with an irregular smooth patch on the vertex and a smooth line extending forward from it to midway between the antennal bases. Antennae dull, the surface of all the segments rather rugose and pubescent, the basal segment nearly as wide as it is long, slightly sinuate on the lower side, the second segment about as wide as it is long and half as long as the first, the third segment a little longer than the first and a little wider than the second, 4th not quite as long and not quite as narrowed at the base as the 3rd, 5th to 10th similar to the 4th but a little larger, 11th similar to these but obtusely pointed at the apex.

One specimen is 9.5 mm. long, the other 8 mm. Both are labelled "Perth, W. Australia".

The type and paratype are in the British Museum.

Ametalloides has some resemblance in appearance to *Ametalla*, but is obviously stouter; it also looks rather like "*Duboulaia*" *rugosa* Baly, but has much more prominent eyes.

18. *Ametalla* Hope.

The three species at present described under this genus are all from Western Australia. Of these, *A. spinolae* Hope and *A. stenodera* Lacordaire are represented by fairly abundant material in the British Museum and the Hope Department, including the types, but *A. w-nigrum* Westwood is represented solely by the type, which now consists of a single elytron. From the coloration and sculpture of this it is hardly possible to separate *w-nigrum* from *stenodera*, nor does the original description give much assistance. I append a key to separate *spinolae* and *stenodera*. Lacordaire (1845) and Chapuis (1874) have stressed the affinities of the present genus towards the DONACIINAE; *Ametalla* is certainly one of the more highly modified Sagrini, and its wing-venation makes some approach to that of *Donacia*, but according to Mr. G. E. Bryant (who has collected both the chief species himself) it is not of aquatic or sub-aquatic habits. It is arguable that the DONACIINAE could be included as a tribe of the SAGRINAE, as suggested by Chen (1940); to do this would entail abandoning the structure of the ligula in favour of the aedeagus as the main

group character in the adult (this in turn would exclude *Aulacoscelis* from the group), while the definition of the group by larval characters would be rendered very much more difficult. An at least equally good case could be made out for the inclusion of the BRUCHIDÆ and MEGALOPODINÆ.

1. Head and pronotum more shining, pubescence inconspicuous, punctuation in parts scattered; surface of pronotum smoothly rounded; elytra more shining, less densely punctured; larger (length 8.5–11.5 mm.); general form more elongate; hind femora more elongate, their greatest width much less than half their length *spinolae* Hope.

Head and pronotum dull, densely and rugosely punctured and with conspicuous pubescence; pronotum with irregular depressions, a large and rather deep one in the middle line about one-quarter of the way from the base, another shallower one about two-thirds of the way from the base, and a small but sharp elliptical one on each side of the disc slightly behind the middle; elytra duller, more closely punctured; size smaller (7–8.5 mm.); form less elongate; hind femora more inflated, their greatest width about equal to half their length *stenodera* Lacordaire.

19. *Atalasis* Lacordaire.

This genus, with a single species, is the sole representative of the Sagrini in the Neotropical region. To a certain extent it may be regarded as an annectant form linking the specialised Ethiopian–Oriental *Sagra* with the main body of the tribe, for example the genus *Mecynodera*; if this annectant form did not exist one would be tempted to place *Sagra* in a special tribe apart from the Australian forms. The sexes differ slightly in the structure of the apical abdominal sternite, and according to Reineck (1913) also in the colour of the elytra, which he says are yellower and duller in the male. Monros (1943) gives a good account of the genus *Atalasis*, with descriptions of varieties of *A. sagroides* and figures. I have a single record of its habits (Hayward 1942) in which it is said to occur on cotton and on wild Malvaceous trees. It is to be noted that *Atalasis sagroides* occurs well outside the tropics, in climatic conditions more like those of the Australian forms than the tropical jungles favoured by species of *Sagra*.

20. *Sagra* Fabricius.

One may reasonably regard the present genus as the most highly evolved of the Sagrini; as evidence for this may be cited the highly developed coloration, the glabrous lower as well as upper surface, the reduced wing-venation, the elaborate secondary sexual characters of the males, the relatively numerous species of the genus, etc. Moreover, the species of *Sagra* form part of the highly evolved Ethiopian and Oriental faunas, while most of the other genera are confined to that menagerie of relicts, Australia. The peculiar modifications of the males of *Sagra* would appear to be connected with the process of copulation; unfortunately there appear to be no published records on this point. Generally speaking, males of this genus have the first visible abdominal sternite depressed along the middle line, with the depression more or less markedly pubescent; this depression seems to be a coadaptation to the convexity of the elytra of the female, and the pubescence would probably enable the sternite to slip more easily over the latter. The femora and tibiae of the hind legs of the male are nearly always considerably modified, suggesting that the insect uses them to hold the female during copulation. This is a matter which I

think would repay investigation by both African and Indian entomologists, especially as the Ethiopian species generally have a type of secondary sexual character rather different from that of the Oriental ones, suggesting some difference in the mode of copulation. These secondary sexual characters are very useful in classifying the species of *Sagra*; an unfortunate result of this is that in many cases single female specimens can scarcely be determined accurately. A paper with morphological figures of *Sagra femorata* Drury has already been published (Maulik 1941); in addition I have previously figured the metendosternite in the same species. The former paper also summarises what is at present known of the habits of the genus, which may roughly be stated as follows:—The larvae of species of *Sagra* live in the stems of more or less woody tropical Dicotyledons, excavating irregular chambers and often causing swellings of the stem; pupation takes place within the larval chamber. The only subdivision of the genus yet proposed is that of Weise, who recognises two subgenera, *Sagra* and *Tinosagra* Weise, the latter being distinguished by a modification of the prosternal intercoxal process; the practical and zoogeographic subdivision is into Ethiopian and Oriental species, which can as a rule be separated morphologically, though I do not know of any single character which can be relied on for this purpose. There appear to be no species of *Sagra* occurring in Asia Minor or the islands of the Indian Ocean, so the geographical division is quite clear-cut. However, I have constructed a single key for both groups of species, partly to make it possible to determine specimens without a reliable locality label, and partly to make evident the complex interrelationships of the African and Asiatic forms. In this genus, more than in any other dealt with here (except perhaps *Syneta*), the problem "What is a species?" becomes acute. In most of the species size, coloration, to some extent sculpture and even proportions vary more or less notably, and even the secondary sexual characters of the males, so largely used to separate species hitherto, vary considerably with the size of the specimen. Maulik (1941) has sunk a considerable number of the Oriental "species" as subspecies or races of *S. femorata*; I have followed him in this but have perhaps been somewhat inconsistent in keeping separate many not very much better characterised African forms. With these latter, once one begins to doubt the validity of the existing "species" it is difficult to know where to stop—there are all degrees of distinctness from the almost subgeneric as shown in *S. javeti* to the extremely weak as seen for instance in the *Tinosagra* "species." I do not accept Weise's group as a primary subgenus, my reason being that *S. murrayi* and *S. tristis* are in every respect except the character stressed by Weise typical African *Sagra*, and incidentally a new species I describe below looks exactly like *S. murrayi* but has not the modified prosternal process. To my mind a subgeneric division should be one that goes very far back, near to the root of the origins of the genus. In the key below I have indicated what seem to me possible subgeneric divisions with suggested names and indications of types.

1. Pronotum very distinctly punctured, the punctures about as large as the facets of the compound eye; form usually relatively short and broad, pronotum shaped more or less as in *stevensi* (fig. 32). Prothorax without a deeply recessed longitudinal groove just below the anterior tubercles 2.
- Punctuation of pronotum, if present, extremely fine 8.
2. Form rather elongate and narrow; front angles of the prothorax with an impressed but not recessed longitudinal line below the tubercles; extreme apices of the elytra rather abruptly truncate in both sexes;

hind femora in the male with a long ovate densely pubescent depression in the basal half below; chiefly blue. Oriental. (Fig. 34.)

[Subgenus *Prosagra* subgen. n. type *S. jansoni* Baly] *jansoni* Baly.

Form much shorter and broader; front angles of pronotum without such an impressed line; hind femora of male without such pubescent depressions; apices of elytra not appreciably truncate

[Subgenus *Sagrina* subgen. n. type *S. carbunculus* Hope] 3.

3. 1st abdominal sternite of male with a tract of pubescence along the middle line; hind femora in male without pubescence along the lower surface; South African *javeti* Baly.

1st abdominal sternite in male without a median tract of pubescence; hind femora of male with pubescence present along lower surface (never in such a clearly marked patch as in *jansoni*); Oriental 4.

4. Prothorax and elytra except the humeri dull blackish, densely shagreened, humeri bright metallic coppery, hind legs in male characteristic (fig. 27) *humeralis* Jacoby. 5.

Prothorax and elytra shining, metallic 5.

5. Elytra with the sutural margin differently coloured from the rest; hind legs in male characteristic (fig. 28), with the inner groove of the hind tibiae densely pubescent throughout, the hind tibiae without a spur-like preapical process *mouhoti* Baly. 6.

Elytra unicolorous; hind legs in male different 6.

6. Elytral punctuation closer and more uniform, hind tibiae in male (fig. 30) without a spur-like preapical process. Rarely blue . . . *carbunculus* Hope.

Elytra smoother, punctures very diffuse near base; hind tibiae in male with a spur-like preapical process. Chiefly blue or green 7.

7. Apex of the mesosternum in the male normal, transverse and convex; hind femora of male less strongly broadened apically, the second tooth of the lower edge much stronger than the first. Generally larger and more highly coloured *fulgida* Weber.

Apex of mesosternum in the male horseshoe-shaped, depressed in the middle; hind femora of male more broadened apically, the second tooth of their lower edge hardly larger than the 1st. Usually smaller and less highly coloured *petelii* Lacordaire.

8. Without a recessed longitudinal groove below the tubercles of the front angles of the pronotum; elytra usually with 8 or 9 more or less regular rows of punctures; hind femora in male usually with an elliptical excavation filled with dense pubescence close to the base of the lower side (subgenus *Orthosagra* subgen. n. type *S. bicolor* Lacordaire). African 9.

With a recessed longitudinal groove below the anterior tubercles of the pronotum; elytra without regular rows of punctures; hind femora of male never with such pubescent excavations (subgenus *Sagra*, type *S. femorata*). Oriental 26.

9. Pronotum broader, of characteristic shape (fig. 32); hind femora in male with a large elongate pubescent excavation extending about two-thirds of the way from the base along the postero-ventral edge; 1st abdominal sternite in the male impunctate and scarcely depressed along the middle line 10.

Pronotum narrower; 1st abdominal sternite in the male always more or less punctured and pubescent along the middle line; pubescent excavation of the hind femora, if present, not so long 11.

10. Elytra highly polished, colour more or less bronzy. West African *senegalensis* Baly.

Elytra rather dull, colour usually bluish or greenish. East African *stevensi* Baly.

11. Hind femora in the male without a pubescent excavation near the base, in the female with the lower edge distinctly serrulate throughout and the apical fifth somewhat raised with a more or less distinct tooth at the beginning of the raised part. Male: hind tibiae greatly thickened towards apex. Colour usually amethyst or violet, rather dull, elytra with small but distinct punctures in 10 more or less regular rows; middle femora simple in both sexes. West African . . . *amethystina* Guérin.
Hind femora in male with a basal excavation filled with bright fulvous pubescence 12.
12. Middle femora of male not at all toothed below 13.
Middle femora of male with a distinct, usually sharp, tooth towards the apex of the lower side 17.
13. 1st abdominal sternite in male with only a very slight development of pubescence along the middle line, chiefly in the posterior half; not occurring in Madagascar 14.
1st abdominal sternite in the male with a dense tract of pubescence along the middle line. Madagascar 16.
14. 1st abdominal sternite in male closely punctured in the middle; head and prothorax usually bluish, elytra reddish or greenish bronzy. East and South Africa *bicolor* Lacordaire.
1st abdominal sternite in the male with only a few scattered large punctures along the middle line, colour uniformly more or less bluish. West African 15.
15. Hind tibiae of the male with a small tooth on the antero-ventral edge near the apex *signoreti*.
Hind tibiae of the male with a long antero-ventral spur near the apex *cyanea* Dolman.
16. Elytra rather dull, less distinctly striate, of the same colour as the rest of the body; general body form less stout *urania* Lacordaire.
Elytra more shining, with very distinct striae, more or less reddish, rest of body bluish; form stouter *bontempsii* Fairmaire.
17. Prosternal intercoxal process normal, bent downwards at the apex; elytra rarely with strong transverse wrinkling 18.
Prosternal intercoxal process sharply raised posteriorly, then abruptly truncate at the apex; elytra always with evident transverse wrinkling; pronotum normally shaped; chiefly north of the Equator (= subgenus *Tinosagra* Weise) 24.
18. Pronotum broader, shaped more or less as in *stevensi* (fig. 32) but with the anterior angles more strongly projecting. East Africa. Elytra with strong transverse wrinkling *neavei* sp. n.
Pronotum normally shaped, front angles less prominent; elytra without marked transverse wrinkling 19.
19. Posterior tibiae of the male without a spur-like antero-ventral projection near the apex, sometimes with a blunt tooth 20.
Posterior tibiae of male with a spur-like outgrowth near the apex of the antero-ventral edge 23.
20. Posterior tibiae of the male quite simple 21.
Posterior tibiae of the male with a distinct tooth near the apex of the antero-ventral edge 22.
21. Posterior femora of the male with two small teeth near the apex of the lower edge. East Africa *johnstoni* Gahan.
Posterior femora of the male with 1 large preapical tooth on the lower edge. Madagascar *coeruleata* Lacordaire.
22. Elytra with quite regular rows of punctures in the basal two-thirds, hind femora in male with a strongly raised dorsal keel towards the apex, hollowed along its front margin. East Africa *ferox* Baly.

- Punctuation of the elytra rather irregular near the base; hind femora in male without a strong dorsal keel. West Africa . . . *ladonis* Lacordaire.
23. Elytra with strong quite regular punctured striae, general form rather narrow, colour piceous with very little metallic sheen. E. Africa
nitidiventris Fairmaire.
 Elytral striae distinct but weaker, general form broader, more or less metallic in coloration *S. nitidiventris* var. *metallica* var. n.
24. Elytra smoother, the transverse wrinkling weak, not masking the fine rows of punctures. West Africa *tristis* Fabricius.
 Elytra less smooth, the rows of punctures masked by the strong transverse wrinkling 25.
25. Transverse wrinkling and rows of punctures on the elytra finer, elytra appearing duller to the naked eye. E. Africa . . . *murrayi* (*galinieri*) Baly.
 Elytra more coarsely sculptured, appearing more shining to the naked eye. West African *dohrni* Baly.
26. Hind femora in the male with an obtuse tooth before the middle of lower edge as well as the usual preapical one, hind tibiae in the male with the inner groove densely pubescent and with a large triangular process near the base as well as the sharper one near the apex. Elytra and pronotum in both sexes entirely impunctate, rather dull and blackish except for a strip along the suture, broadest near the base, which is coppery or greenish *buqueti* Lesson.
 Hind femora in the male without a tooth on the lower edge before the middle, hind tibiae without dense pubescence in the inner groove and without a triangular process near the base; elytra with a few large punctures in both sexes, colour different 27.
27. Male: posterior femora with preapical tooth bifid, posterior tibiae with fairly strong preapical spur (fig. 35) *femorata* Drury.
 Male: preapical tooth of posterior femora trifid, preapical tooth of hind tibiae weak or absent *tridentata* Weber.

Sagra neavei sp. n.

General form almost exactly as in *S. murrayi* except that the prothorax is relatively wider with more prominent front angles (fig. 33). Upper surface unicolorous, rather dull, metallic bronzy to greenish. Head with scattered small punctures, becoming dense and rather rugose around the frontal grooves, surface between the punctures dull and shagreened. Pronotum also dull and shagreened with extremely fine scattered punctures, except for the front of the tuberosity of the front angles which is shining, the basal margin also slightly shining. Elytra with rather regular rows of fairly strong punctures, the striae somewhat masked by a rather strong irregular transverse wrinkling as in *S. murrayi*, which is stronger in the basal half; the surface of the elytra, particularly the basal half, is rather less dull than that of the pronotum, the humeri being particularly shining and sculptured with very fine close punctures. Prosternal intercoxal process simple, no trace of the modification found in *S. murrayi* and its allies. Hind femora of the male not extending far beyond the apex of the elytra, fairly straight and not very much inflated, with a single stout preapical tooth below (fig. 29), and a rather long elliptical pubescent excavation extending about two-fifths of the way from the base along the lower side; hind tibiae in the male somewhat curved, grooved along the outer side, without preapical processes. Middle femora in the male with a sharp tooth in the apical half below. 1st visible abdominal sternite in the male with a well-marked median tract of pubescence which is broadest in front. In the female the hind femora have a weakly bicuspid raised area near the apex of the lower edge, the hind tibiae are less curved than in the male and their outer edges are sharply keeled, while the middle femora are somewhat angled below.

Length: male (7 specimens) 18–21 mm., female (8 specimens) 17.5–22 mm.

Type: a male. All specimens in the British Museum.

Localities: N.E. RHODESIA (Serenje district), NYASALAND, S. RHODESIA (MASHONALAND); all the specimens seem to have been caught in November, December, and January, chiefly in the last two months.

S. neavei seems to be a well-characterised and distinct species; the variety of *nitidiventris* which I have described as var. *metallica* is quite as distinct as several of the forms which, following older authors, have been named as species in my key; the question of the limits of species in these forms can scarcely be resolved without a knowledge of their biology and genetics which is totally lacking at present. For this reason, among others, my key is purely provisional and its main purpose is to draw the attention of others to such classificatory characters as I have been able to discover in the genus. As regards the general relationships of the species, the most primitive forms seem to be those of the subgenus *Sagrina*; from these the true *Sagra* seem to have been derived by way of forms like *S. jansoni*, while the African *Orthosagra* may have arisen from something intermediate between the latter and *S. javeti*.

GENERAL CONCLUSIONS: PHYLOGENY AND ZOOGEOGRAPHY.

The absence of SAGRINAE from oceanic islands suggests that they are not easily transported over stretches of sea, and should hence be of value in a study of zoogeography; it would also appear that the group includes the most primitive of the CHRYSOMELIDAE, so that all the other groups of the family should be derivable from it, and the origins of the present group will be equivalent to the origins of the entire family. From a study of zoogeography (including the palaeontological data), it should be possible to deduce the approximate age of the group and its various tribes, and their areas of origin. From these data, combined with those of comparative morphology, physiology and genetics, one may eventually be able to deduce the phylogeny of the group with reasonable certainty. All that can be done under this head in the present state of knowledge is to speculate on very insufficient data; my only excuse for indulging in speculation on these matters here is that I may thereby draw the attention of other students to certain features of the SAGRINAE which should repay further investigation.

The SAGRINAE are almost cosmopolitan but entirely absent from New Zealand; from this one may reasonably conclude that the group is not as old as, for instance, Reptilia-Rhynchocephalia, and in fact can hardly have originated earlier than the Triassic period. On the other hand, the strong development of the group in Australia, by exclusively endemic genera (disregarding the probably recent incursion of the Indo-Malayan *Sagra* in the north), makes it probable that the group came into existence before the separation of Australia from the main land-masses of the world. This would point to the Cretaceous period, and probably the Lower Cretaceous, as the lower limit of its age. With the exception of one or two species of the anomalous genus *Syneta*, and perhaps of the rather specialised *Carpophagus* (if the records (Walker 1906) of its occurrence on *Macrozamia* are significant), all members of the group seem to occur only on Angiospermae. This makes it probable that the ancestral forms of the group fed on Angiosperms, and if so, the group must have originated after Angiosperms appeared. The period of origin of the true flowering plants is still disputed—the oldest undoubted remains of them seem to be from the Lower Cretaceous deposits of Greenland, but many palaeobotanists consider that the group really arose during the Jurassic

period (Seward 1931). The evidence, such as it is, seems to suggest that the SAGRINAE arose about or a little before the beginning of the Cretaceous period. Accepting this as a hypothesis, one must seek for the origins of the SAGRINAE (and of the family CHRYSOMELIDAE) in some group which already existed at that time. In considering the definition of SAGRINAE, two families were mentioned which cannot easily be excluded by the definition—these are the CERAMBYCIDAE and the BRUCHIDAE. In the latter family, as far as I know, neither the adult nor the larvae show any primitive characters not found in the SAGRINAE; moreover BRUCHIDAE, even more than SAGRINAE, seem to be exclusively attached to Angiospermae. The essential characters separating BRUCHIDAE from SAGRINAE, in both the adult and the larval state, are clearly derivative (the pedunculate mentum in the adult, the shield-shaped hypopharyngeal sclerome in the larva); it is more reasonable to suppose that BRUCHIDAE arose from SAGRINAE than vice versa. In the family CERAMBYCIDAE there are certain characters found which do, however, appear to be more primitive than those of the SAGRINAE—such for example as the presence of urogomphi in the larvae of some of them and of contiguous anterior tendons in the metendosternite of the adult (Crowson 1938, 1945); also many of the CERAMBYCIDAE (including, be it noted, forms with the primitive morphological features just mentioned) feed on Gymnosperm trees. The single genus *Parandra* has comparatively few species with a wide but discontinuous geographical distribution including Australia and the Holarctic region, which suggests that it is practically as old as the entire group SAGRINAE. As far as the morphological and zoogeographic evidence goes, it seems quite possible that SAGRINAE come from Cerambycid ancestors. Incidentally, the basic wing-venation of the CERAMBYCIDAE seems almost the same as that of SAGRINAE (Saalas 1936). One of the differences commonly stressed between the CERAMBYCIDAE and CHRYSOMELIDAE is that larvae of the former family feed in woody stems, whereas the latter family are regarded as basically leaf-feeders. But if the habits of Chrysomelid larvae are considered more critically, it becomes apparent that larvae with exposed leaf-eating habits are found only in the most specialised groups—the CHRYSOMELINAE, some of the GALERICINAE–HALTICINAE, and the more modified of the CASSIDINAE. In the CHRYSOMELINAE, the genus *Timarcha* has a more primitive type of aedeagus than the rest, and its larva has correspondingly a more hidden mode of life; in the CASSIDINAE the most primitive forms are presumably those with the “Tortoise-beetle” shape least developed—the annectant forms linking this subfamily with the HISPINAE—and in these the larvae lead a fully concealed life beneath the closely adpressed leaf bases of Palm trees. Larvae of Camptosomata conceal themselves within portable cases, EUMOLPINAE larvae lead a subterranean life feeding on roots, in the CRIOCERINAE a covering of excrement is usual, and DONACIINAE larvae live on or in the stems of water plants, under water. Finally, in the SAGRINAE, the larva of *Sagra* feeds in semi-woody stems, and that of *Orsodacne* mines in young shoots of trees (note also that Bruchid larvae live inside seeds). These facts seem to me quite consistent with the theory that CHRYSOMELIDAE come from ancestors the larvae of which were borers in the stems of trees, and that the general trend of evolution in the family has been away from this habit and towards that of feeding on soft green tissues. There is some analogy in this to the development from the concealed fungus-eating type of larva found in the Cryptophagid–Erotylid group through root-frequenting forms (e.g. *Hyperaspis*) to the completely free-living Aphid-eating larvae in the higher COCCINELLIDAE, the larvae of which incidentally look

remarkably like those of CHRYSOMELINAE and probably have similarly distasteful properties.

I now turn to consider the relationship of the SAGRINAE to other Chrysomelid groups—the BRUCHIDAE, as already indicated, seem to be a direct offshoot of some early Sagrine type, the leading features of which have been conditioned by a larval life in seeds. The Camptosomata seem to have come from a very early type of SAGRINAE, probably by way of the MEGALOPODINAE (of the larvae and habits of which nothing seems to be known as yet); the basic type of wing venation in Camptosomata is almost the same as that of the Sagrini. The EUMOLPINAE are not at all easy to separate sharply from SAGRINAE, and all appearances suggest that the former group is an offshoot of the latter; once again the wing venation in the larger forms shows very little difference in the two groups (cf. figs. 9, 10). The genus *Syneta* shows a considerable approach to the EUMOLPINAE (and is said to have a root-feeding larva); *Psatyrocerus* has a little more similarity to EUMOLPINAE and a little less to SAGRINAE and I think it may actually be included in the former group. A direct link from SAGRINAE to CHRYSOMELINAE is suggested by the fact that *Aulacoscelis* was originally referred to the latter group (Chevrolat 1843), shares its venational pattern, and has an aedeagus much like that of *Timarcha* (Sharp and Muir 1912). The similarities of DONACIINAE to SAGRINAE are well known (see my notes on *Ametalla*), and the former group could easily have come from the latter. The group GALERUCINAE—HALTICINAE, although I do not know of any annectant form connecting them with the SAGRINAE, may likewise be directly derived from the latter. The basic wing-venation of these Trichostome groups is the same as that of CHRYSOMELINAE and *Aulacoscelis*, and it is possible that all these forms share a common origin—this is implied by Chen (1940), who places CHRYSOMELINAE, HALTICINAE and GALERUCINAE together in a single group. The type of metendosternite found in the Trichostomes is not derivable from that of the CHRYSOMELINAE, but both could well have come from the type found in *Aulacoscelis*. There remain the Cryptostomes; here again I am not able to cite any form which could be taken as intermediate between them and the SAGRINAE, but there seems to be no special difficulty in deriving the CASSIDINAE and HISPINAE from the group I am studying. The wing-venation in the more primitive of the Cryptostomes (e.g. Alurnini) does not differ greatly from that of the SAGRINAE (see Kempers 1923); the metendosternite in *Aspidomorpha* is more modified than that of *Sagra* but of basically the same construction. The characteristic strongly deflexed head of the Cryptostomes is of course a derivative feature. It seems possible that the primitive Cryptostome types may have been attached to Palm trees, as are such forms as Alurnini and *Himatidium* today (Bondar 1940): the Palmae are Monocotyledons, and the tendency of modern systematic botanists is to regard these as ultimately derivable from Dicotyledons—also, the primitive types of Cryptostomes are not found in Australia, so most lines of evidence seem to agree in suggesting a more recent (late- or post-Cretaceous) origin for the HISPINAE—CASSIDINAE than for SAGRINAE.

I now consider the individual tribes composing the SAGRINAE. *Aulacoscelini* have a single recent genus with 12 or more species in Central America. The marked systematic isolation of this genus indicates that there must have been other genera connecting it with the rest of the SAGRINAE at some time; this puts *Aulacoscelis* in the category of relicts, and makes it not very safe to base conclusions on its present-day distribution. Presumably it must have originated either in the Neotropical or in the Holarctic region. A Holarctic

origin seems more probable *a priori*, as the Glacial epoch certainly drove many subtropical organisms southward from North America, and since then the species of *Aulacoscelis* (which are probably attached to trees) may have been prevented from spreading northward again by the increasing aridity of the southern parts of the United States of America. Also, the CHRYSOMELINAE-Timarchini, which I have mentioned above as being possibly derived from Aulacoscelini, are a Holarctic group. *Hornibius* is a more obviously relict form than *Aulacoscelis*; its present distribution might lead to its being classified among Antarctic forms; however, the entire absence of related forms from New Zealand argues against such a conclusion, whereas *Plastorsodacne* and *Psathyrocerus* which occur farther north in Chile appear to have some relationship to *Hornibius*. *Cucujopsis* may have some relationship to *Hornibius*, but until further specimens are collected so that it becomes possible to dissect a specimen I do not think its affinities can be usefully discussed. The Orsodacnini are to all appearances a primarily Holarctic group; the Ethiopian-Oriental subgenus *Pedrillia* of *Zeugophora* seems to be derived from the Holarctic forms, and furthermore the Ethiopian *Pedrillia* seem to have come from the Oriental ones and not directly from the Holarctic. It is my opinion that the Chilean *Orsodacne unicolor* Blanchard and *O. tessellata* Blanchard will, like *O. grandis* Philippi, prove not to belong in the Orsodacnini: according to a recent communication from Dr. R. Paulian of the Paris Museum, the unique type of *Orsodacne splendida* Montrouzier from Woodlark Island (New Guinea) must be presumed lost. For the Sagrini, the term Gondwanian suggests itself; the alternative that must be considered is that the group might be originally cosmopolitan but now extinct in the Holarctic region. But as against the latter view there is the entire absence of the group from North and Central America (where many relicts of old Holarctic groups survive) and from the extensive Tertiary fossil faunas of Europe and North America.

Finally, I think it worth pointing out that as far as known all CHRYSOMELIDAE outside the SAGRINAE have two or more apical teeth in the larval mandible. If my theory, as sketched above, is correct, this character must have evolved more than once in the evolution of the family. Possibly the straight-edged type of mandible is better adapted for dealing with firm and massive tissues, while mandibles with toothed apices are more suited for feeding externally on leaves and stems. The straight-edged larval mandible, be it noted, is found also in all BRUCHIDAE and the lower types of CERAMBYCIDAE and CURCULIONIDAE.

Published Morphological Data on SAGRINAE.

The only general account I have seen of the structure of a beetle belonging to this group is that by Maulik (1941) of *Sagra femorata*. Several authors have included species from the group in comparative morphological studies; of these I have seen the following:—

The head-capsule and tentorium of *Syneta ferruginea* described and figured by Stickney (1923); the wing-venation of *Zeugophora subspinosus* and *Z. flavipennis*, also *Sagra femorata* and an African species figured by Kempers (1923); the metendosternite of *Sagra femorata* and *Orsodacne lineola* figured by Crowson (1938), of *Carpophagus banksiae* figured by Crowson (1945); the aedeagus of *Orsodacne nigriceps*, *Carpophagus banksiae*, *Diaphanops westermanni*, and *Sagra amethystina* figured by Sharp and Muir (1912), of *Orsodacne atra* by Powell (1941); the wing-folding pattern of *Zeugophora kirbyi* by Forbes (1926).

In addition, a few morphological figures are given in the course of systematic works, for instance Baly (1860) figures the mouth-parts, legs, abdominal sternites, etc., of *Cheiloxena insignis*; Mjöberg (1917) figures the tarsus of *Pseudotoxotus vestitus*; Reineck (1913) figures the aedeagus of *Rhagiosoma madagascariense* and *R. grossum*; and Chen (1940) figures the wing-venation of *Sagra* and *Orsodacne*.

Jacoby (1908) figures the hind legs of males of *Sagra petelii* and *S. multipunctata*.

The larval structure of *Sagra*, *Orsodacne* and *Zeugophora* is illustrated by Böving and Craighead (1931); Maulik gives a good figure of the larva of *Sagra femorata*, with details of the mouth-parts and the structure of the spiracles.

ACKNOWLEDGEMENTS.

My best thanks are due to Mr. N. D. Riley, Keeper of the Department of Entomology at the British Museum, for putting the full facilities of that institution at my disposal and thereby making the present study possible; I am also deeply obliged to Prof. G. D. Hale Carpenter, who sent to me for study the relevant material from the Hope Department. In carrying out the actual work I have received very much valuable advice and assistance from Mr. G. E. Bryant of the Imperial Institute of Entomology; others who have generously helped me in various ways in preparing this paper are Dr. H. E. Hinton, Dr. F. van Emden, Dr. K. G. Blair, Mr. S. Maulik, Mr. J. Balfour-Browne, and Miss O. Tassart. The entire study has been carried out while I have been serving in the Royal Air Force, and has been materially facilitated by the Service authorities. The final preparation of this paper has been partly carried out in the Castle Museum, Norwich, and for this my thanks are due to Miss E. V. Barnard and Mr. E. A. Ellis.

BIBLIOGRAPHY.

(Note: references given in Clavareau's volume of the *Coleopterorum Catalogus* are not repeated here except where specifically cited in the text.)

- ACHARD, J., 1914, *Macrozeugophora* gen. nov. *Bull. Soc. ent. Fr.* **83**: 289.
 —, 1916, *Bruchomima* gen. nov. *Bull. Soc. ent. Fr.* **85**: 47.
 BALLY, J. S., 1860, *Trans. ent. Soc. Lond.* (n.s.) **5**: 254.
 BELLER, S., and HATCH, M., 1932, The Coleoptera of Washington: CHRYSOMELIDAE. *Univ. Wash. Publ. Biol.* **1**: 65-144.
 BLACKBURN, T., 1888, *Pseudotoxotus* gen. nov. *Proc. Linn. Soc. N.S.W.* (2) **3**: 1470-72.
 BOISDUVAL, J. A., 1835, Faune de l'Océanie. *Voyage de l'Astrolabe (Zoologie)* **2**: 530.
 BONDAR, G., 1940, Notas entomologicas de Bahia VI. *Rev. ent. Rio de J.* **11**: 842-61.
 BÖVING, A. G., and CRAIGHEAD, F. C., 1931, An Illustrated Synopsis of the principal larval forms of the Coleoptera. *Ent. Amer.* (n.s.) **11**: 1-351.
 BRÈTHES, J., 1928, Chilean CHRYSOMELIDAE. *Rev. Chil. Hist. nat.* **32**: 204-7.
 BRIDWELL, J. C., 1932, The subfamilies of the BRUCHIDAE. *Proc. ent. Soc. Wash.* **34**: 100-6.
 BRISLEY, H. R., 1927, Review of the tribes Orsodacnini and Criocerini in Western North America. *Pan-Pac. Ent.* **4**: 54-60, 114-19.
 BRYANT, G. E., 1943, New Species of African *Zeugophora*. *Ann. Mag. nat. Hist.* (10) **1**: 245-8.

- CHAPUIS, F., 1873, in Lacordaire *Genera des Coléoptères* 10.
- CHATTERJEE, N. S., and BHASIN, G. D., 1936, *Ind. For. Rec.* (n.s.) 1 : 243-318.
- CHEN, S. H., 1934, Sur la position systématique du genre *Timarcha* Latr. *Bull. Soc. ent. Fr.* 39 : 35-9.
- , 1940, Attempt at a new classification of the Leaf Beetles. *Sinensia* 11 : 451-81.
- , 1942, A Synopsis of the SAGRINAE of China and Indo-china. *Sinensia* 13 : 105-7.
- CHEVROLAT, A., 1843, in Orbigny *Dict. univ. Hist. Nat.* 2 : 338.
- CHUJO, M., 1932, Studies on the CHRYSOMELIDAE of the Japanese Empire. II. *Trans. nat. Hist. Soc. Formosa* 22 : 338-45.
- , 1937, *Trans. nat. Hist. Soc. Formosa* 27 : 146-51.
- CLAVAREAU, H., 1913, SAGRINAE, DONACIINAE, ORSODACNINAE. *Col. Cat.* 51.
- CROWSON, R. A., 1938, The met-endosternite in Coleoptera. *Trans. R. ent. Soc. Lond.* 89 : 397-416.
- , 1945, Further studies on the met-endosternite in Coleoptera. *Trans. R. ent. Soc. Lond.* 95 : 273-310.
- FAIRMAIRE, L., 1885, *Ann. Soc. ent. Fr.* (6) 5 : 62.
- , 1888, *Miss. Sci. Cap Horn* 6 : 60-1.
- FORBES, W. T. M., 1926, The Wing-folding patterns of the Coleoptera. *J. N.Y. ent. Soc.* 34 : 42-68, 91-139.
- GRESSITT, J. L., 1942, Plant Beetles from South and West China. I. *Lingnan Sci. J.* 20 : 271-87.
- HAYWARD, K. J., 1942, Primera Lista de Insectos Tucumanos Perjudiciales. *Misc. Pub. Est. exp. agric. Tucuman* 1 : 1-110.
- JACOBY, M., 1890, Descriptions of new species of Phytophagous Coleoptera. *Entomologist* 23 : 84.
- , 1897, *Proc. zool. Soc. Lond.* 1897 : 244.
- , 1903, SAGRIDAE in Wytsman *Genera Insectorum* 14.
- , 1908, *Fauna of British India. Coleoptera* : CHRYSOMELIDAE I.
- KEMPERS, K. J. W. von B., 1923, Abbildungen von Flügelgeäder der Koleopteren. *Ent. Mitt.* 12 : 71, 162.
- KUNTZEN, H., 1915, Zur Kenntnis der Sagra-arten. *Arch. Naturg.* 80 (A) (9) : 45-61.
- LACORDAIRE, T., 1845, *Monographie des Coléoptères Phytophages*.
- LEA, A. M., 1917, Results of the South Australian Museum expedition to Strzelecki and Cooper's creeks : Coleoptera. *Trans. R. Soc. S. Austr.* 41 : 489-630.
- , 1918, Notes on some Miscellaneous Coleoptera, with Descriptions of New Species. IV. *Trans. R. Soc. S. Austr.* 42 : 272.
- MARCU, O., 1939, Die Stellung der Bruchiden im System. *Folia Zool. Hydrobiol.* 9 : 370-4.
- MAULIK, S., 1941, Biology and Morphology of the SAGRINAE. *Ann. Mag. nat. Hist.* (11) 7 : 235-54.
- MJÖBERG, E., 1917, Results of Swedish Scientific Expedition to Australia, 1910-1913. 14. *Ark. Zool. Stockholm* 11 (3) : 19.
- MONROS, F., 1943, La familia SAGRIDAE en Sud-Amerika : el genero *Atalasis* Lac. *Rev. Soc. ent. Argent.* 11 : 411-22.
- PIC, M., 1914, *Rhagiosoma obscurithorax* sp. nov. *L'Échange* 30 : 21.
- , 1917, *Pedrilliomorpha* gen. nov. *Melanges exotico-ent.* 41 : 9.
- POWELL, E. F. 1941, Relationships within the family CHRYSOMELIDAE as indicated by the male genitalia. *Amer. Midl. Nat.* 25 : 148-95.
- REINECK, G., 1913, Beitrag zur Kenntniss der Sagriden Gattungen *Rhagiosoma* und *Atalasis*. *Deuts. ent. Z.* 1913 : 300-9.
- SAALAS, U., 1936, The wing-venation and phylogeny of CERAMBYCIDAE. *Ann. Zool. Soc. zool.-bot. Vanamo* 4 : 1-198.
- SEWARD, A. C., 1931, *Plant Life throughout the Ages*. Cambridge.
- SCHAEFFER, C., 1933, Short studies of CHRYSOMELIDAE. *J. N.Y. ent. Soc.* 41 : 297.

- SHARP, D., and MUIR, F., 1912, The comparative anatomy of the male genital tube in Coleoptera. *Trans. ent. Soc. Lond.* **1912** : 477-642.
- STICKNEY, F. S., 1923, The head-capsule in Coleoptera. *Illinois biol. Mon.* **8** : 1-104.
- WALKER, J. J., 1906, Antipodean Field Notes III. *Ent. mon. Mag.* (2) **17** : 22-7.
- WEISE, J., 1905, Neue Afrikanische CHRYSOMELIDAE und COCCINELLIDAE. *Deuts. ent. Z.* **1905** : 33-54.

INDEX TO LETTERING OF FIGURES.

L = labrum; E = eye; A = antennal socket; S = scape of antenna; P = pubescent tract; G = frontal grooves; Li = ligula; M = mentum; Sm = submentum; TG = transverse grooves of prothorax; Pr = anterior angles of prothorax; Se = setae on the basal tubercles of prothorax; St2 = mesosternum; C2 = mesocoxa; T2 = its trochantin; Es2 = mesepisternum; Em2 = mesepimeron; El = elytron; Ep = epipleuron of elytron; S3 = metasternum; Ts = transverse suture of metasternum; Es3 = metepisternum; C3 = metacoxa; T = anterior tendon of met-endosternite; F = ventral median flange; V = ventral process; Lp = lateral processes of ventral process; 4 = 4th tarsal segment; R = radius; M = media; C = cubitus; X = the spurred cross-vein between R and M; W = anal cell (Wedge cell of Forbes).

Vol. 97. Part 5. Pp. 117-148, 6 figs.

20th August, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

	PAGE
X COLLIN, J. E. The British genera and species of OSCINELLINAE (Diptera, CHLOROPIDAE) . . .	117-148, 6 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 10s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.	} <i>Vice-Presidents</i> .
C. B. WILLIAMS, M.A., D.Sc.	
H. B. WILLIAMS, LL.D.	

A. WELTJ, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.	CAPT. R. A. JACKSON, R.N.
J. W. EVANS, M.A., D.Sc.	MISS C. E. LONGFIELD.
G. FOX-WILSON, N.D.H.	SIR GUY A. K. MARSHALL, K.C.M.G.,
R. M. GREENSLADE.	D.Sc., F.R.S.
FRANCIS HEMMING, C.M.G., C.B.E.	G. E. J. NIXON, B.A.
H. E. HINTON, B.Sc., Ph.D.	J. F. PERKINS, B.Sc.

Registrar :

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.	W. RAIT-SMITH.
FRANCIS HEMMING, C.M.G., C.B.E.	O. W. RICHARDS, M.A., D.Sc.
H. E. HINTON, B.Sc., Ph.D.	

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.	J. SMART, B.Sc., Ph.D.
B. M. HOBBY, M.A., D.Phil.	W. H. THORPE, M.A., Sc.D.
J. F. PERKINS, B.Sc.	

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.	O. W. RICHARDS, M.A., D.Sc.
K. G. BLAIR, D.Sc.	N. D. RILEY (<i>Secretary</i>).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.	A. M. MASSEE, D.Sc.
E. A. COCKAYNE, M.A., M.D., F.R.C.P.	THE HON. MIRIAM ROTHSCHILD.
CAPT. R. A. JACKSON, R.N.	W. H. THORPE, M.A., Sc.D.
COL. F. A. LABOUCHERE.	N. D. RILEY (<i>Secretary</i>).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. **British National Committee for Biology** (Royal Society).
Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.
Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.
2. **Local Committee of Management of Wicken Fen.**
Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].
3. **National Trust for Places of Historic Interest or Natural Beauty.**
Mr. H. M. Edelsten, O.B.E., appointed 1944.
4. **New Forest Association.**
Mr. W. Fassnidge, appointed 1934.
5. **New Forest Joint Committee.**
Mr. W. Fassnidge, appointed 1939. *Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.*
6. **Royal Meteorological Society. Phenological Committee.**
Dr. C. B. Williams, M.A., D.Sc., appointed 1937.
7. **Biology War Committee.**
Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.
8. **Council for the Promotion of Field Studies.**
Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.
9. **Joint Bioclimatic Committee.**
Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

THE BRITISH GENERA AND SPECIES OF OSCINELLINAE (DIPTERA, CHLOROPIDAE)

By J. E. COLLIN.

Manuscript received 14th May, 1945.

(Read 16th January, 1946.)

WITH 6 TEXT-FIGURES.

MEMBERS of the subfamily OSCINELLINAE of the CHLOROPIDAE are mainly distinguished by having the costal vein extended to end of discal vein, in very rare exceptions it is at least extended to midway between the ends of cubital and discal veins, while the latter vein is not much fainter than the former, and a vibrissal bristle (even if only a small one) is stronger than other hairs on mouth-edge. It is one of the groups in British Diptera in which vast changes have been made in recent years, both in the number of known species and their generic arrangement. Verrall's *List* of 1901 mentioned only four genera and twelve species; the following pages will deal with 24 generic divisions and over 80 species. It is evidently a group in which evolutionary changes have been recently active, with the result that generic distinctions have not become sharply defined, nor species very stable; in the case of some species it will remain impossible, without much laborious, detailed, and accurate, work on life-histories, similar to that attempted by Mesnil in 1936 (*Les Insectes nuisibles aux plantes cultivées* 2), to decide whether the numerous small differences indicate true species, biological races, seasonal forms, or are mere haphazard variations; these remarks particularly apply, so far as the British fauna is concerned, to the *frit*-group of *Oscinella*, but there are other cases among the European fauna. Wherever possible in the genus *Oscinella* I have endeavoured to make my identifications recognisable by basing them on bred specimens. By far the most important recent work on the OSCINELLINAE is that of Duda, though some of its shows signs of hasty publication without the necessary critical revision; he has, however, laid what appears to be a sound foundation for future work.

The following Table of Genera, though mainly based on Duda's researches, includes certain changes which are obviously necessary, and some modifications which, it is believed, will enable the genera to be more readily recognised.

Table of Genera.

- 1(44). Arista not thickened or flattened, and, if pubescent, hairs not dense except (rarely) when they are white.
- 2 (3). Antennae separated at base by a wide pollinose "keel" which is continued in same width (or almost as wide) down face, and may widen out below. Vibrissal angles in no way prominent . . . *Lipara* Mg.
- 3 (2). If antennae are separated at base it is only by a small triangular (often not pollinose) "keel," which, when continued down face, is still very narrow, and often only linear.
- 4(25). Face in profile with more angulated or only narrowly rounded vibrissal angles, which usually project beyond level of eyes; in doubtful cases

- frontal triangle dusted (often very densely), and orbital bristles more than 4-5 on each orbit; or thoracic pubescence much more dense and universal (not arranged in lines) and disc of scutellum with numerous hairs.
- 5(14). Frontal triangle shining, without any trace of dust, and usually large.
- 6(13). Radial vein longer, ending in costa at a point vertically well beyond end of postical vein.
- 7(10). Orbital bristles very numerous (more than 12), short and fine, very little differentiated from other frontal hairs. Frontalia dull.
- 8 (9). Epistoma not produced beyond vibrissal angles. Proboscis shorter. Frontal triangle with small upcurved hairs on its disc away from side-margins *Calamoncosis* End.
- 9 (8). Epistoma produced beyond vibrissal angles. Proboscis very long and geniculate. Frontal triangle without hairs except at side margins *Siphonella* Mcq.
- 10 (7). Orbitals less numerous (about 8) and stronger. Frontalia shining.
- 11(12). Facial "keel" more broadly triangular above and extending down to clypeus, completely separating the very deep antennal foveae *Polyodaspis* Duda.
- 12(11). Facial "keel" narrowly triangular above and fading away into a flat whitish area on face above clypeus where the antennal foveae merge into one another *Goniopsita* Duda.
- a(b). Head in profile longer with vibrissal angles more produced beyond front margin of eyes, and jowls wider. More resembling profile of *Polyodaspis* *Goniopsita* sens. strict.
- b(a). Head in profile shorter with vibrissal angles not produced beyond front margin of eyes, and jowls narrower subgen. *Lasiambia* End.
- 13 (6). Radial vein very short, ending nearly opposite end of postical *Siphunculina* Rdi.
- 14 (5). Frontal triangle dusted (often very densely) and never very large.
- 15(24). Thorax without three deeply impressed and punctate longitudinal lines, or without impressed rows of shining punctures.
- 16(17). Species with coloration more like that of *Chlorops*, scutellum, humeri and most of pleurae yellow; thoracic disc often with narrow yellow stripes *Trachysiphonella* End.
- 17(16). Unicolorous species or at least without the above yellow markings.
- 18(19). Vibrissal angles projecting beyond front of frons, face often very short and proboscis long and geniculate (*Siphonella*-like), in doubtful cases sternopleurae shining *Oscinimorpha* Lioy.
- 19(18). Vibrissal angles not projecting beyond front of frons, face not so much shorter than frons, and proboscis not long. If vibrissal angles are slightly projecting pleurae are extensively dull.
- 20(21). Meso-, ptero-, and sterno-pleurae dusted; often an anteroventral spur to hind tibiae *Aphanotrigonum* Duda.
- 21(20). Pleurae mainly shining; no spur to hind tibiae.
- 22(23). Head from in front much wider than deep with jowls less vertical. Scutellum longer with marginal bristles arising from tiny warts *Oscinisoma* Lioy p.p.
- 23(22). Head from in front very little wider than deep with jowls more vertical. Scutellum shorter with no tiny warts *Conioscinella* Duda.
- 24(15). Thorax with three deeply impressed, punctate, lines *Tricimba* Lioy.
- 25 (4). Face in profile with vibrissal angles more broadly rounded and never more prominent than front margin of eye. Face often retreating. In doubtful cases either frontal triangle shining (at any rate in part), or if dusted, orbitals not more than 4-5 on each orbit.

- 26(27). Radial vein very long, last two costal segments together about one-half or less than one-half length of previous segment. Arista almost bare
Dicraeus Lw.
- 27(26). Radial vein shorter, last two costal segments together more than one-half length of previous segment.
- 28(29). Head much deeper than long (compressed from front to rear). Head bristles long. Arista distinctly pubescent. Shining black species
Mimogaurax Hall.
- 29(28). Head not conspicuously compressed from front to rear.
- 30(31). Yellow species with black disc to thorax. Head bristles long. Eyes and arista distinctly pubescent, *Gaurax*-like . . . *Botanobia* Lioy.
- 31(30). Black or grey species of different structure.
- 32(35). Thorax more dorso-ventrally flattened than usual, sometimes conspicuously so. Head also somewhat flat.
- 33(34). Thorax and scutellum coarsely punctate. Wings short and broad, sometimes scarcely longer than abdomen . . . *Oscinisoma* Lioy p.p.
- 34(33). Thorax and scutellum only very finely punctate. Wings narrow and much longer . . . *Eribolus* Beck.
- 35(32). Thorax not dorso-ventrally flattened. Head more normal.
- 36(39). Frontal triangle dusted, even if only very slightly, if (rarely) with large shining patches (*Tropidoscinis nigrifrons*) front margin of frons convex.
- 37(38). Head more as in couplet 4 (25), with frons more sloping and vibrissal angle more acute. Thoracic pubescence more universal
Conioscinella Duda.
- 38(37). Head more square with frons less sloping and vibrissal angle more rounded. Thoracic pubescence less dense and more in rows
Tropidoscinis End.
- 39(36). Frontal triangle shining or only dusted between ocelli, or (rarely) at angles.
- 40(43). No hairs on the shining part of frontal triangle though it is outlined by hairs.
- 41(42). Face more perpendicular. Thoracic pubescence more scanty and arranged more or less in lines. Front margin of frons concave
Oscinella Beck.
- 42(41). Face retreating. Thoracic pubescence more universal *Lioscinella* Duda.
- 43(40). Hairs on the shining part of frontal triangle at sides *Hapleginella* Duda.
- 44 (1). Arista flattened and pubescent, or at least with dense black pubescence; if doubtful about arista pubescence one or two orbital bristles on each side of frons stronger than usual.
- 45(48). More than two orbital bristles each side of frons and these shorter.
- 46(47). Third antennal joint normally rounded. Flies more resembling *O. frit*
Melanochaeta Bezzi.
- 47(46). Third antennal joint much produced at upper corner. Flies more like species of *Elachiptera* . . . *Gampsocera* Schin.
- 48(45). Only two (sometimes only one) stronger orbital bristles each side of frons . . . *Elachiptera* Mcq.

Lipara Meigen

- 1(4). Longitudinal stripes of pubescence on thorax with hairs orientated towards the right in one stripe, towards the left in the next, producing a ridged appearance.
- 2(3). Pubescence yellowish. Palpi and third antennal joint mainly black
lucens Mg.

- 3(2). Pubescence whitish. Palpi and third antennal joint mainly yellow
similis Schin.
 4(1). Pubescence on thorax not arranged in stripes and uniformly orientated
rufitarsis Lw.

L. lucens Mg. causes the well-known large terminal galls on reeds, which are very common.

L. similis Schin. also lives in the terminal part of reeds without, however, causing any obvious swelling. I have found it at both Wicken and Chippenham Fens (Cambs.).

L. rufitarsis Lw. causes a more obvious gall on reeds than *similis*, but not so large a one as that caused by *lucens*. My specimens were bred by Dr. K. G. Blair from galls collected on the coast of Devon, and in June 1943 I caught a female at Chippenham Fen (Cambs.).

Dr. Duda has made two mistakes in connection with this species, first in placing it in the genus *Calamoncosis* when its facial structure and larval habits prove it to be a *Lipara*; and secondly in considering it to be a synonym of *Gymnopoda tomentosa* Mcq. So long ago as 1911 I pointed out that the size quoted by Macquart for *tomentosa* as well as his description of "Noire à duvet jaune" prove that his species can have been only *L. lucens*. This mistake of Duda's may be due to the fact that Perris described the life-history of *rufitarsis* Lw. under the name *Gymnopoda tomentosa* Mcq. On the other hand, Duda was quite correct in stating that the species identified by Enderlein as *rufitarsis* Lw. (the type of Enderlein's genus *Calamoncosis*) was not Loew's species but the *Lipara minima* of Strobl.

Calamoncosis Enderlein.

Stizambria End. (with type *aprica* Mg.) is a synonym.

- 1(4). Frontal triangle at most only a little more than half length of frons and then only one strong posterior notopleural bristle.
 2(3). Frontal triangle only half length of frons. Two strong posterior notopleural bristles. Halteres yellow. Female ovipositor strongly chitinated, laterally compressed, style-like *laminiformis* Beck.
 3(2). Frontal triangle about $\frac{2}{3}$ length of frons. Only one strong posterior notopleural bristle. Halteres dark. Female ovipositor normal *aprica* Mg.
 4(1). Frontal triangle almost to front of frons.
 5(6). Wings not whitish. Scutellum longer. Thorax more densely punctate. Tip of front femora yellow *minima* Strbl.
 6(5). Wings whitish. Scutellum semicircular. Thorax less densely punctate and more shining. Tip of front femora dark . . . *duinensis* Strbl.

All the species occur in marshy districts, *aprica* and *duinensis* more particularly in coastal marshes, while *minima* appears freely when breeding out *Lipara lucens*. They all exhibit great variation in size.

C. laminiformis Beck. was described from Canary Island specimens having entirely black antennae, dark tarsi, and clear wings, whereas in British specimens the basal joints and base of third joint of antennae, and usually all tarsi, are obviously yellow, and wings slightly brown. However, specimens with darkened tarsi do occur in this country in company with the more usual form, and have been bred from the same foodplant by Mr. Goodliffe. I therefore use the name *laminiformis* for the British species in spite of their different antennal coloration. It is common in marshy situations and both Mr.

Goodliffe and I have bred it from *Glyceria aquatica*, the larvae feeding gregariously on the ensheathed inflorescence of this grass.

C. aprica Mg. is the species recorded as British under the name *tristis* Lw. which is a synonym. *C. colligata* Beck. is a not uncommon variety with an adventitious crossvein connecting the radial and cubital veins.

C. duinensis Strbl. though primarily a sea-coast species, and also occurring (like some other coastal species) at Barton Mills (Suffolk), has been taken in Chippenham Fen (Cambs.). The specimens from this last locality have the basal antennal joints darker (almost black), no trace of chestnut-brown coloration to frontal triangle, and tarsi not so clearly yellow. These differences are very similar to those between British *laminiformis* Beck., and the typical Canary Island form.

Siphonella Macquart.

This genus, at one time used for all OSCINELLINAE with long geniculate proboscis, is now restricted to *oscinina* Fln. only, a species of wide distribution which I take freely at Barton Mills (Suffolk) in August by sweeping conifers, but I also have records from Herts, Oxon, Hereford and Glamorgan.

Duda incorrectly attributed to this species a record by Schwangart (1906) of parasitism. Schwangart in *Z. wiss. Insektenbiol.* 11 : 105 actually stated that the species bred from the cocoons of *Aranea virgata* Hahn were "nahe verwandt, aber nicht identisch mit *Siphonella oscinina* Fall." Schwangart's species was almost certainly the *Conioscinella halophila* Duda referred to later in this present paper under that genus.

Polyodaspis Duda.

Duda left this and allied genera in a somewhat fluid condition; that his characterisation is not the same as mine is shown by the fact that he included *sulcicollis* Mg. in his genus *Goniopsita*. The grouping of species suggested by me appears to be a natural one as far as the British fauna is concerned.

- 1(2). First basal cell twice as wide at radio-cubital node as at end of cell.
Scutellum with a pair of closely approximated long apical bristles and a number of very short marginal spines *ruficornis* Mg.
2(1). First basal cell very little wider at radio-cubital node than at end.
Scutellum with apical bristles wide apart and only 2-3 successively shorter bristles on each side-margin . . . *sulcicollis* var. *anglicus* var. n.

P. ruficornis Mcq. This is the *Siphonella nucis* Perris and may not be an indigenous British species because the only specimens I have seen were bred from walnuts bought in London and probably imported.

P. sulcicollis Mg. is said to be a very variable species. I first became acquainted with the species when I took a dozen specimens at Dungeness (Kent) on 5th August, 1937. These exhibit very little variation, and as they do not appear to answer to any described form of *sulcicollis*, they may be known as :—

Polyodaspis sulcicollis var. *anglicus* var. n.

♂♀. Antennae with basal joints brown, third joint brown above but yellowish beneath especially on inner side; front of frons, keel between antennae, and front half or more of jowls, tawny-brown. All hairs and most bristles on head whitish. Palpi yellow, with very short and inconspicuous dark hairs. Abdomen with rather long and conspicuous whitish hairs. Legs mainly black with front tibiae paler (especially at both ends), and all tarsi

brownish-yellow, but sometimes front tibiae almost all yellow and middle tibiae also considerably yellowish, and tarsi distinctly yellow. Wings with a whitish tinge and yellowish veins.

The typical form was described by Meigen as having head, antennae and legs shining black, frons dull black with shining triangle, and wings clear. The var. *anglicus* answers better to the description of *sulcicollis* given by Becker than that given by Duda, and might pass as Duda's *amicalis* Beck., but Duda does not appear to have seen the type of *amicalis* (one male from Algiers) which was described by Becker as having very narrow jowls (narrower than third antennal joint) and scutellum with whitish hairs and white bristles. Duda's *amicalis* (three specimens from Tunis) are described by him as having jowls wider than third antennal joint, but narrower than in *palposa*, and scutellum black-haired without mention of colour of bristles. Our species has the wider jowls of Duda's *amicalis*, but while the hairs on thorax and scutellum are dark, the bristles or macrochaetae are nearly all whitish.

Goniopsita Duda.

- 1(2). First basal cell narrower (as in *P. sulcicollis*). Frons wider with very numerous scattered short bristles arising from small punctures *palposa* Fln.
 2(1). First basal cell widened at middle (as in *P. ruficornis*). Frons narrower with only a few small bristles *parcepilosa* sp. n. ♀.

G. palposa Fln. is a little known British species. My specimens were all captured by Col. Yerbury, some at Nairn on the north-east coast of Scotland and others at Porthcawl (Glamorgan) on the Welsh coast.

Goniopsita parcepilosa sp. n.

♀. Head very much as in *palposa* but vibrissal angles still more produced; palpi yellow, not so produced or dilated, and antennae yellow with only a slight browning about base of arista. Frons rather narrower and more shining without the glistening grey appearance in some lights of the frontalia in *palposa*; the frontalia also with decidedly fewer tiny bristles. Jowls all shining, and tawny, not glistening whitish below the eyes as in *palposa*. Thorax less densely haired and consequently rather more shining, two strong posterior notopleural bristles. Scutellum flat on disc as in *palposa* but a little narrower compared with its length, smooth and bare about middle of base. Abdomen with less numerous hairs, and some (on hindmargins of tergites at sides) longer. Legs paler than in *palposa* but front coxae tawny-brown like front and other femora; tarsi, front tibiae except for a narrow band about middle, and middle tibiae except for a broader band, yellow. Wings clear, veins yellowish; first basal cell twice as wide opposite radio-cubital node as at end of cell; cubital vein straight, last section of discal vein slightly convex below. Halteres dark. Length about 2 mm.

Described from a female taken by Francis Jenkinson at Cambridge in October 1920.

Goniopsita subgen. *Lasiambia* Enderlein.

- 1(2). Tibiae distinctly pale at both ends. Palpi yellow, not very stout and with short hairs. Jowls with only a single row of hairs on the narrowly darkened lower margin. Scutellum coarsely punctate and rather dull. Last abdominal segment only about $1\frac{1}{2}$ times length of previous one *brevibucca* Duda.

- 2(1). Tibiae almost entirely black. Palpi brownish and rather stouter, with more distinct (though still short) hairs. Jowls with hairs in more than a single row. Scutellum not so punctate and consequently more shining. Last abdominal segment twice length of previous one

baliola sp. n.

G. (L.) brevibucca Duda. There are two British species of the *Lasiambia* group of which I, somewhat doubtfully, recognise one as *brevibucca* Duda, the doubt being mainly due to Duda's statement that the palpi are "sehr gross." This species is not uncommon in July on the windows of my house here at Newmarket (Suffolk), but it also occurred in company with the next species in August 1934 at Moccas Park (Hereford), and I found it in Denny Wood, New Forest (Hants), in June 1939.

Goniopsita (*Lasiambia*) *baliola* sp. n.

♂. Closely resembling *brevibucca*, and probably often confused with that species, differing as follows: long axis of eye rather more diagonal; jowls more extensively darkened below with hairs in more than one row (irregularly biserial); palpi rather stouter, more often brownish-yellow and with rather longer hairs. Thoracic pubescence less dense and consequently thorax rather more shining; scutellum less punctate and with shorter pubescence. Abdomen rather less dusted and the apparent last (fifth) pregenital segment longer, as long as previous two together. Legs with tibiae darker, only base of front tibiae yellowish, others practically entirely black. Wings usually distinctly brownish on costal half. Halteres pale.

♀. Resembling male but fifth abdominal tergite not quite so long. Length about 1.5 mm.

The darker tibiae, and more shining, less pubescent scutellum, with (in addition to the apical pair) two, more distinct, lateral marginal bristles on each side, appear to be particularly reliable characters.

Described from three males and a female taken in Moccas Park (Hereford) in August 1934, and a male at Cothill (Berks) in July 1939. Two pairs (rather immature) bred in May and June 1908 from material taken from an ulcerous elm tree at Chippenham (Cambs.) appear to belong to the same species.

Siphunculina Rondani.

Under *Opinion* 46 of the Int. Comm. Zool. Nomenclature this generic name of Rondani's is available for use in spite of the fact that a species, named as belonging to it, was not described. This species, *brevinervis* Rdi., having been claimed to be the same as *Siphonella aenea* Mcq., which agrees with the generic characters given by Rondani for *Siphunculina*, Macquart's species becomes the type of Rondani's genus.

S. aenea Mcq. is not a common British species. My only records are from Hereford (Cusop) and Sussex (Crowborough, Lewes and Etchingham), the specimens having been taken by G. H. Verrall, F. Jenkinson and C. G. Lamb. Quite recently a female has been captured in Woodditton Wood (Cambs.).

Trachysiphonella Enderlein.

The species added to the British List in 1911 as *Siphonella pumilionis* Bjerk., but which is now known not to be Bjerkhander's species but the *Oscinis pumilio* of Zetterstedt, was included by Duda under *Conioscinella*, but in 1935 was made the type of a new genus of the above name by Enderlein, and this genus appears to be as well founded as most of Duda's genera. The single

representative and type is subject to marked variation, and Duda mentions three distinct forms. The first of these, var. *flavella* Zett. (which according to Seguy's note on Meigen's type of *Chlorops pygmaea* must be that species), is the palest, with humeri yellow, only mesopleura with a distinct dark patch, and yellow legs. This form was taken by me in some numbers at West Stow (Suffolk) in June 1922, and in these specimens the head in profile has the vibrissal angles less produced than usual, but a male taken on the Fleam Dyke (Cambs.) in July 1937, while having the same coloration, had the vibrissal angles more produced. The other forms have distinct dark patches on the ptero-, hypo- and sterno-pleurae (in addition to that on mesopleurae). Of these the var. *ruficeps* Mcq. has the thoracic stripes confluent, or only very narrowly separated behind, the dark ocellar area larger and more triangular, and legs considerably darkened; it occurs in the paddock behind my house here at Newmarket (Suffolk). Typical *pumilio* Zett. is larger than any of the other forms (1.25-1.33 mm.), the thoracic dark stripes narrowly separated in front, darkened ocellar triangle not so large as in *ruficeps*, crossveins not quite so close together, and at least front femora extensively darkened behind. This I have taken sparingly at Barton Mills (Suffolk). Finally, specimens occur on the Devil's Dyke and Fleam Dyke, near Newmarket (Cambs.), which may be only pale forms of *ruficeps* with thoracic stripes not confluent, smaller dark ocellar area and yellow legs, the crossveins (as in *ruficeps*) closer together than in typical *pumilio*.

Oscinimorpha Lioy.

The type of this genus is *O. obliqua* Mcq. from the north of France. Enderlein (1935) professed to recognise this species from Italian specimens, of which he stated *Siph. minutissima* Strbl. was probably only a variety, although the outer crossvein in *minutissima* is not particularly oblique. Duda (1933) thought that *obliqua* Mcq. might be a species of *Goniopsita*. I doubt the correctness of either of these identifications and consider it more probable that Macquart's species was the one recognised by Duda as *cincta* Mg., a species apparently known to Macquart only from Meigen's description. However, as *minutissima* Strbl. belongs to a group which can be distinguished from *Conioscinella*, I am using the generic name *Oscinimorpha* for this group rather than burden the nomenclature with a new name. Probably a more natural arrangement would be to retain *albisetosa* Duda and *sordidissima* Strbl. in a new genus, and include *arcuata* Duda and *minutissima* Strbl. in *Conioscinella*, which they more resemble in facial structure, though the vibrissal angles are more produced.

- 1(4). Face very short and *Siphonella*-like, median keel extended to mouth-edge, completely isolating the deep antennal foveae.
- 2(3). All hairs and bristles on head, thorax and abdomen whitish, pleurae extensively dull. Front of frons, face, jowls and palpi yellow
albisetosa Duda var. *hollandica* Duda.
- 3(2). All hairs and bristles black. Sternopleura shining. Head and palpi black
sordidissima Strbl.
- 4(1). Face longer, median keel very narrow, not completely extended to mouth-edge and not nearly so steeply dividing the antennal foveae.
- 5(6). Legs entirely yellow in both sexes. Sternopleura with a small dusted patch on upper margin. Radial vein longer *arcuata* Duda.
- 6(5). Legs with all femora and ring on hind tibiae dark in male, all entirely yellow in female. Sternopleura entirely shining above. Smaller species with shorter radial vein *minutissima* Strbl.

O. albisetosa Duda. The type form was described as having entirely pale yellow legs, whitish arista, and yellowish wings. Our specimens agree with the var. *hollandica* in having all femora extensively darkened and tibiae with dark rings (in both cases more so in male than in female), arista at most somewhat yellowish towards tip, and wings clear with brownish veins. This is not uncommon at sea-coast localities in Suffolk, Essex, Kent, Sussex, Hants and Dorset.

O. sordidissima Strbl. is a much darker insect which I, on one occasion, found on the grassy cliffs at Sheringham (Norfolk) in August.

O. arcuata Duda, is the species added to the British List in 1911 as *Siphonella longirostris* Lw. Loew's species described from the female only would appear to have the front mouth-edge more produced, longer proboscis, and some darkening to hind femora and tibiae.

O. minutissima Strbl. This species has occurred at Felixstowe (Suffolk), Kirtling (Suffolk), and on the Fleam Dyke (Cambs.), and at St. Merryn (Cornwall).

Aphanotrigonum Duda.

The only species placed in this genus by Duda was *trilineatum* Mg. (*annulifera* Ztt.), but there are several other species which are more closely related to *trilineatum* than to *frontella* and must therefore be placed in *Aphanotrigonum* rather than in *Conioscinella*. A useful character in British species indicating this relationship to *trilineatum* is the more extensively pollinose pleurae.

- 1 (2). Three to five brown stripes down disc of thorax. . . . *trilineatum* Mg.
- 2 (1). Thorax without distinct brown stripes.
- 3 (4). Jowls below eyes much wider than third antennal joint. All bristles on head and thorax very short and whitish *meijerei* Duda.
- 4 (3). Jowls not wider than third antennal joint. At least some bristles on head and thorax black and distinct.
- 5 (8). Scutellar bristles short and apical pair not much wider apart than postocellar bristles; if wider apart, short and fine.
- 6 (7). Bluish-grey species with thorax and scutellum distinctly punctate. Third antennal joint evenly rounded and darker, especially on outer side. Two posterior notopleural bristles *griseum* sp. n.
- 7 (6). Yellowish-brown species, less punctate on thorax and scutellum. Third antennal joint with somewhat produced upper corner and paler, especially on outer side. Only one posterior notopleural
brunneum sp. n.
- 8 (5). Scutellar bristles longer and apical pair wider apart and stronger.
- 9(10). Four anterior legs entirely yellow *fasciella* Ztt.
- 10 (9). All coxae and femora dark.
- 11(12). Distinct yellow hindmargins to all abdominal tergites. A small antero-ventral spur to hind tibiae. Prothoracic episterna shining
femorella sp. n.
- 12(11). No yellow hindmargins to tergites in male and only very narrow ones in female. No anteroventral spur to hind tibiae. Prothoracic episterna dull *inermis* sp. n.

A. trilineatum Mg. is a common marsh or fenland species in the spring, and may be found during the winter in heaps of cut sedge or litter. The somewhat projecting front margin of frons (convex when seen from above) of this species is common to all the species of the genus, and forms an additional distinction from species of *Conioscinella*.

A. meijerei Duda is at present known only from the Norfolk coast (Palling and Yarmouth).

***Aphanotrigonum griseum* sp. n.**

Resembling *trilineatum* in having two equally strong posterior notopleural bristles, but differing from that and all other species in having 8-10 marginal scutellar bristles, all very short.

♂. Head yellow with occiput, vertex, and frontal triangle (extending half-way down frons) dull grey. All hairs and bristles very short and pale except for the ocellar, vertical, and first (posterior) one or two orbital bristles, which are black; a few tiny hairs arising from minute punctures on the frontal triangle away from the sides; orbital bristles numerous and very short, distinguished with difficulty (except for the 1-2 black upper ones) from other frontal pubescence. Antennae with basal joints yellow, the rounded third joint dark brown but yellowish beneath about base. Jowls yellow, about as wide as third antennal joint is deep, the tiny hairs on lower margin in several rows; vibrissae very short.

Thorax including all pleurae dusted bluish-grey; pleurae somewhat shining on the concave areas in front and behind against which the front and middle femora press, but even these areas usually have a dusted middle patch. Thoracic disc and scutellum minutely punctate with microscopic hairs arising from the punctures. Humeral, prescutellar dorso-central, and marginal scutellar bristles, all short; one anterior and two posterior notopleurals, and one rather longer postalar bristle, all black (*trilineata* appears to be the only other British species with a distinct second postalar bristle).

Abdomen broad and flat, ground colour more brownish than thorax, especially about base, also rather less dusted and consequently more shining. No pale hindmargins to segments. Pubescence very sparse and scattered, short, and pale.

Legs black, or brownish-black, dusted greyish; trochanters, extreme tip of femora, base and tip of tibiae, and all tarsi, tawny-yellow. Hind tibiae with a very small dark antero-ventral spur.

Wings longer than abdomen, faintly brownish with dark brown veins; last section of discal vein more than three times length of previous section (between crossveins). Halteres yellow or pale brownish-yellow.

Length 1.5-1.75 mm. (♂), sometimes 2 mm. (♀).

Described from four males and two females taken at Aldeburgh (Suffolk) in May 1910. Another female was found at Bawdsey (Suffolk) in April 1912, and Col. Yerbury took a female at Wareham (Dorset) in September 1906.

***Aphanotrigonum griseum* var. *curtipenne* var. n.**

♀. Differing from normal form chiefly in much shorter wings (length measured from humeral crossvein to tip compared with that of typical form of same size being in proportion of 68:98), and last section of discal vein only about twice length of previous section. Third joint of antennae paler about base, even on outer side; frons more extensively (more than upper half) greyish, and abdominal pubescence dark.

A female taken by myself at Barton Mills (Suffolk) at the end of April 1933, and two females by Mr. James Murray near Gretna (Dumfries-shire) in May 1937 and April 1938.

***Aphanotrigonum brunneum* sp. n.**

Brownish species with only one strong posterior notopleural bristle, no distinct dark anteroventral spur to hind tibiae, orbital bristles almost as long and distinct as verticals and similarly black in colour, and prothoracic episterna dusted.

♂. Head in shape and colour much as in *griseum*, but dark parts browner, frons flatter,

and eyes with long axis rather more diagonal. Antennae yellow, third joint slightly brownish above and upper outer corner slightly produced. Jowls as in *griseum*.

Thorax dull, browner on disc than in *griseum* especially on prescutellar area, and this coloration tends to spread forward in 3-5 narrow stripes. Scutellum flat and greyer, apical marginal bristles finer and much longer than in *griseum*, also not so close together, but not so far apart as in *fasciella*, only one other distinct pair of shorter lateral bristles, the third (basal) pair being only microscopic. Humeral and prescutellar dorsocentral bristles not so noticeably short as in *griseum*.

Abdomen longer and narrower than in *griseum* and not flattened, brownish-grey and only slightly shining, hind margins of tergites very narrowly pale grey. Pubescence sparse and scattered, pale.

Legs mainly brownish-black and dusted greyish, but front tibiae mainly yellowish-brown, middle tibiae of this colour at both ends, hind tibiae less distinctly so; tarsi, especially middle tarsi, also yellowish-brown.

Wings slightly yellowish-brown, veins not very dark. Halteres yellow.

♀. Resembling male, abdomen ending in a telescopic ovipositor with long slender terminal papillae.

Length about 1.25 to nearly 2 mm.

Described from a pair taken on Hayling Island (Hants) on 15th June 1938. Col. Yerbury had previously taken one male and two females at Walton-on-Naze (Essex) in August 1907 and another female in July 1909.

A. fasciella Zett. Duda placed *fasciella* Ztt. as a synonym of *cinctella* Ztt. but this latter was described as having entirely pale legs, while *fasciella* has the hind legs darkened. I have found no variation in this respect in our British species, and cannot, in the circumstances, accept the synonymy as proved.

Our British *fasciella* ♂ has yellow antennae with only a pale brownish patch about insertion of arista; clypeus entirely yellow; legs yellow, front legs (including coxae) entirely yellow, middle femora very slightly darkened beneath, hind femora more extensively darkened, hind tibiae dark about middle with a distinct small black anteroventral spur at tip. Abdomen with the combined first and second segments yellowish with three rounded dark patches across middle on upperside, 3rd to 5th tergites with fairly wide yellowish hindmarginal bands, the anterior margin of each band somewhat undulating. Female similar but darkening beneath middle femora often very faint, and the sixth abdominal tergite yellowish.

It has been taken on the coasts of Suffolk, Essex, Kent and Hants.

Aphanotrigonum femorella sp. n.

Resembling *fasciella* in having only one posterior notopleural bristle, apical scutellar bristles wide apart, and a distinct small dark spur to hind tibiae, but differing as follows:— Basal antennal joints yellowish-brown, third joint rather larger and more extensively brownish on outer side; clypeus darkened; abdominal dark markings more extensive, hindmargins of tergites 3-5 more narrowly pale. Legs much darker, front coxae and all femora dark, front tibiae brownish but yellow about base, middle tibiae with dark band about middle, hind tibiae more extensively darkened, tarsi brownish.

♀. Resembling male but abdominal pale markings often still more restricted or even absent except on hindmargin of 5th tergite, sixth tergite always pale.

Length 1.5-1.75 mm. (slightly larger than *fasciella*).

This species has been found at various coastal localities in Norfolk, Suffolk, Essex, Hants, Kent and Dorset, from June to September inclusive, often in

the same situations as *griseum*, *fasciella*, *inermis* and other sea-coast OSCINELLINAE.

Aphanotrigonum inermis sp. n.

Resembling *femorella* in colour of antennae, clypeus, and legs, and in having only one posterior notopleural bristle, and apical scutellar bristles wide apart, but easily distinguished by the absence of an anteroventral spur to hind tibiae, the dusted prothoracic episterna (in both *femorella* and *fasciella* it is bare and shining) and abdomen usually without pale bands or hindmargins to tergites, except on fifth tergite in female.

About the same size as *femorella*.

This species has occurred at Orford and Butley (Suffolk), Walton-on-Naze and Kirby-le-Soken (Essex), Hayling Island (Hants), and Arne and Studland (Dorset). The shining patch between prothoracic spiracle and base of front coxae must not be mistaken for episternum which lies in front of it.

Oscinisoma Liroy.

This genus was founded upon Macquart's description of *Oscinis vitripennis* Mg. and *O. vindicata* Mg., and the former (which is said to be the same as *O. cognata* Mg.) was selected as genotype by Coquillett. In 1932 Duda described an Oscinellid under the name *germanica*, which he placed in Enderlein's genus *Discogastrella* (founded upon a Brazilian species), and this *Discogastrella germanica* has been recognised as occurring in Britain. *O. cognata* Mg. differs from *D. germanica* in having the frontal triangle shining, not dusted or pollinose, a difference which Duda always considered of generic importance. I find that these two species resemble one another so closely in all other respects that it is impossible to believe that the dusting of the frontal triangle in *germanica* is of greater than specific value in this particular instance.

O. germanica Duda, in addition to the dusted frontal triangle, has larger, longer wings than *cognata* Mg., with thorax rather stouter and not so coarsely punctate on disc. I first caught this species at St. Germans (Cornwall) in May 1914 and later in Darnaway Forest (Elginshire) in June 1934, but it had been taken previously by Dr. J. H. Wood in Herefordshire.

O. cognata Mg. was added to the British List in 1911. Additional county records of its occurrence are Norfolk and Hants.

Conioscinella Duda.

With the removal from this genus of the species of *Oscinimorpha* and those I have placed in the genera *Aphanotrigonum* and *Tropidoscinis*, the species left in *Conioscinella* are reduced to a few resembling the type species *frontella* Fl. in the characters given in my table of genera. I shall deal with the genus *Tropidoscinis* later, but the species described by Duda as *Tropidoscinis gallarum* only differs from *Conioscinella* in having the frontal triangle less densely dusted; in structure of head, number of orbital bristles, arrangement of microchetae on thorax, and other characters, it is a *Conioscinella*, and I therefore include it in that genus.

- 1(2). Thorax shining, not dusted. All bristles and hairs whitish-yellow.
Legs pale yellow. Front of frons and palpi yellow. Antennae darker yellow, slightly brownish above *gallarum* Duda.
- 2(1). Thorax conspicuously dusted.
- 3(4). Abdomen with rather conspicuously long whitish hairs. Scutellum with soft brown hairs on margin as well as bristles. No distinct ventral spur to middle tibiae *halophila* Duda.

- 4(3). Abdomen with shorter hairs. Scutellum with marginal bristles only.
Middle tibiae with distinct dark ventral spur.
- 5(6). Frons yellow with only triangle darkened, all head bristles yellowish.
Jowls rather wider and pale yellow. All legs yellow in both sexes.
Abdomen brownish *sordidella* Ztt.
- 6(5). Frons yellow in front only, head bristles darker. Jowls narrower and
never pale yellow. Legs darkened at least in male.
- 7(8). Femora dark in both sexes, middle tibiae broadly darkened (♂), very
narrowly dark banded (♀). Frontal bristles longer . . . *frontella* Fln.
- 8(7). Femora dark in male only, middle tibiae pale in both sexes. Frontal
bristles shorter *mimula* sp. n.

C. gallarum Duda. A very distinct species associated with *Andricus* galls on oak trees. I have taken it in some numbers on oaks at Barton Mills (Suffolk) in June.

C. halophila Duda is a rather larger, plumper, species, also easily recognised. The pubescence is everywhere rather longer than usual, and the male genitalia with two stout curved shining black lamellae are very distinctive. It has been bred by Mr. A. H. Hamm of Oxford from spider's eggs. I have taken it at Barton Mills (Suffolk), and it is the species recorded by me in 1911 as *Oscinis pratensis* Mg.

C. sordidella Ztt. Duda, probably following Becker, sank this species with some doubt as a synonym of *cinctella* Zett. (*frontella* Fln. of Becker having been proved by Duda to be a mixture of *cinctella* and *frontella*). Our British species cannot be Duda's *cinctella* because it has the sternopleurae shining, not dusted. It is almost certainly the *frontella* var. *flavifrons* of Duda, but it also agrees in every respect with Zetterstedt's description of *sordidella*, the name under which it was added to the British List in 1911.

C. frontella Fln. There is a sexual difference in the colour of the legs, which probably has been responsible for the suggestion that this species is a very variable one. In the male the legs are mainly dark with knees, tips of tibiae, and all tarsi except last joint, yellowish; the front tibiae rather paler (brownish) than others. In the female the legs are paler, with front coxae extensively pale, all trochanters, and middle as well as front tibiae mainly yellowish. Middle tibiae rather stout, especially in male. Palpi always yellow. It is not uncommon in Scotland but is also widely distributed in England and Wales.

Conioscinella mimula sp. n.

Resembling *frontella* but smaller, the legs of male similar in colour to those of female of *frontella*, and of female entirely yellow. Frontal hairs and bristles shorter, hairs on jowls and palpi yellowish. The female differs from the yellow-legged female of *sordidella*, in having a smaller head with upper half or more of frons darkened, frontal and thoracic hairs and bristles not so yellowish, facial orbits and jowls rather narrower and latter never so pale yellow, third antennal joint obviously brownish above.

Length about 1 mm. (♂) to 1.5 mm. (♀).

This species appears to be widely distributed in Britain, having been captured in Cambs., Suffolk, Surrey, Oxford, Hereford, Glamorgan, and Sutherland.

Tricimba Lioy.

It should be noted that the type of this genus is *lineella* Fln. of Macquart because Lioy's work was based upon the description given in Macquart's

Hist. Nat. Ins. Dipt. Macquart's *O. lineella* was not necessarily the same as Fallen's; in fact I feel certain that *lineella* Fln. will prove to be the species Duda called *cincta* Mg. The species Duda called *lineella* does not appear to occur in Northern Europe. Frey records only *T. cincta* (Mg.) Duda from Finland, and Zetterstedt's description of *lineella* Fln. with "scutellum . . . apice saepissime flavum" applies far better to *cincta* (Mg.) Duda. It would be unwise, however, to make any alteration in the use of these names until types have been examined. The two British species are remarkably distinct, indeed it is possible to believe that *cincta* would be more correctly placed in *Conioscinella*.

- 1(2). Only 4-5 orbital bristles; thoracic lines more deeply impressed and the microchaetae between them (intermediate acrostichals of Duda) practically only uniserial; upper basal cell remarkably widened opposite radio-cubital node *lineella* (Fln.) Duda.
- 2(1). Seven or eight fine orbital bristles; thoracic lines less impressed and intermediate microchaetae more than uniserial; upper basal cell not abnormally widened. *cincta* (Mg.) Duda.
 - a(b). Legs in male with front coxae and all femora only partly tawny brown, and only hind tibiae obscured about middle; in female legs entirely yellow *cincta* Mg. (typical).
 - b(a). Legs in male with front coxae and all femora brownish-black with only tips of latter yellowish, and all tibiae partly brown; in females legs as in male of *cincta*
var. *apicalis* v. Ros. (*sulcella* Ztt.).

T. lineella (Fln.) Duda. Our British specimens nearly always have two dark rings on hind tibiae (above and below the posterodorsal sense organ) and answer to the description of *delpinii* Rdi. They often occur in some numbers on windows here at Newmarket (Suffolk).

T. cincta (Mg.) Duda. Both forms of this species are probably more widespread than my captures indicate. I possess var. *cincta* from Cambs. and Suffolk, and var. *apicalis* from Suffolk, Dorset and Cornwall.

Dicraeus Loew.

This is one of the more distinct genera of the OSCINELLINAE and remarkable inasmuch that in some species the costa is not continued to end of discal vein, and the outer crossvein may be missing. The use of these characters and the width of the jowls for subdividing the genus, as has been suggested by Enderlein, is neither natural nor necessary. Synonyms are as follows—*Dicraeus* End. type *ingratus* Lw., *Oedesiella* Beck. type *discolor* Beck., and *Paraoedesiella* End. type *styriaca* Strbl.

In the figures given below of the male hypopygia only the ninth tergite and its appendages are shown.

- 1 (4). Costa not quite extending to end of discal vein.
- 2 (3). Black species with black antennae and legs, conspicuous black palpi, only face and part of jowls yellowish. Outer crossvein present
ingratus Lw.
- 3 (2). Species with yellow front of frons, antennae, front legs, middle tibiae, all tarsi, and part of abdomen. Outer crossvein missing
raptus Hal.
- 4 (1). Costa reaching end of discal vein.

- 5 (6). Pleurae extensively dulled by dust, but not yellowish. Male genitalia smaller. Abdomen brownish, or (especially about base) yellowish. Jowls wide, entirely yellow. Legs extensively darkened, but front tibiae pale *tibialis* Mcq.
- 6 (5). Pleurae extensively shining. Male genital segments large and broad.
- 7 (8). Species resembling *raptus* in general coloration but both humeri and pleurae partly yellowish, outer crossvein present and jowls wider *vagans* Mg.
- 8 (7). Darker species, at least humeri and pleurae not partly yellowish.
- 9(16). Antennae with at least basal joints yellowish or brownish, not black; front of frons, face and jowls usually conspicuously yellowish.
- 10(11). Third antennal joint with slight darkening about base of arista, spreading in female on outer side of joint; front and middle tibiae and all tarsi yellowish; wings rather milk-white. Male genitalia with long club-like side-lamellae or claspers (fig. 2, a) *fennicus* Duda.
- 11(10). Third antennal joint extensively darkened, or at least some darkening on inner side; front and middle tibiae not entirely yellowish.
- 12(13). Third antennal joint on inner side contrastingly dark at tip, yellow beneath about base; only front tibiae yellow. Male genitalia with large, long, dark, claspers (fig. 2, b) *scibilis* sp. n.
- 13(12). Third antennal joint not as above and front tibiae as dark as others; tarsi all darkened. Male genital claspers shorter and broader.
- 14(15). Front of frons and jowls clearly yellow, lower half of jowls not darker and jowls not so wide *vallis* sp. n.
- 15(14). Front of frons and jowls inconspicuously yellowish, and lower half of the wider jowls darkened (compare with *styriacus* Strbl.) *napeus* sp. n.
- 16 (9). Antennae entirely black. Dark species *styriacus* Strbl.

The male genitalia of the first three species are very much alike, with those of *fennicus* and *scibilis* also similar except that the parts are much larger; in the other four species the genitalia again have a general resemblance but with lamellae quite unlike those of the first group.

D. ingratus Lw. was first taken in this country by Col. Yerbury at Walton-on-Naze (Essex) in 1908, then it was found by Mr. Michelmores on the banks of

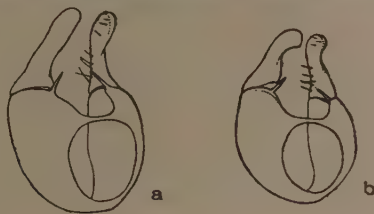


FIG. 1.—a. *D. ingratus*, b. *D. tibialis*.

Wicken Lode (Cambs.) in 1928. The male ninth tergite and appendages are shown in (fig. 1, a). I find it on the Devil's Ditch near Newmarket (Cambs.). All records are for the month of June.

D. raptus Hal. occurs fairly freely in one part of the Forty Acre Wood in Chippenham Fen in July..

D. tibialis Mcq. This species was added to the British List in 1911 (when the front legs instead of front tibiae were stated to be pale), and is described by Duda under the name *pallidiventris* Mcq., but I cannot accept Macquart's

description of "D'un jaune fauve. Thorax noir en dessus; metathorax noir," as correctly applying to our species. Male genitalia fig. 1, b.

D. fennicus Duda. First described by Duda as a variety of *styriacus*; he later in an appendix to his paper (Lindner, *Die Fliegen*, CHLOROPIDAE) considered it a synonym of *nitidus* Wahlg. in spite of the fact that he had previously (under *styriacus*) noted that Wahlgren described *nitidus* as having black antennae, yellowish-brown jowls, and brown palpi. Our British species, which I have taken in Norfolk, Suffolk, Essex and Kent, and Mr. Verrall in Cambs., agrees with Duda's description of his *styriacus* var. *fennicus* but is certainly specifically distinct from *styriacus* Strbl. which is a much blacker

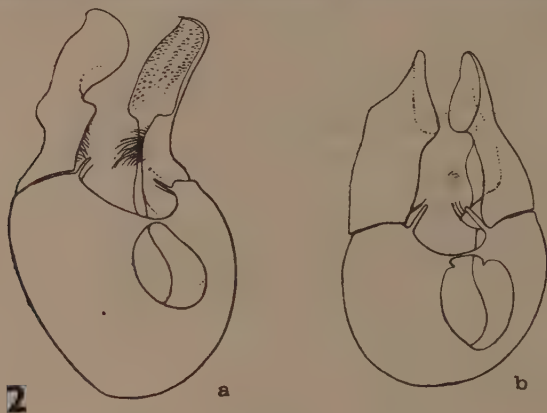


FIG. 2.—a. *D. fennicus*, b. *D. scibilis*.

species with completely different male genitalia. Compare figs. 2, a (*D. fennicus*) and 3, b (*D. styriacus*).

Dicraeus scibilis sp. n.

♂. Superficially resembling *fennicus*, and with similar type of male genitalia but differing as follows:—Front of frons, face, jowls and antennae not so clear yellow, jowls rather narrower, not so wide as third antennal joint, this latter entirely brownish on outer side, yellowish on inner side about base beneath, but contrastingly dark above and at tip. Palpi brownish with conspicuous black hairs. Thorax and abdomen all dark, pleurae extensively shining; genital lamellae dark, not yellow as in *fennicus*. Legs with middle tibiae as dark as hind ones, only front tibiae brownish-yellow; all tarsi brownish. Wings shorter and broader and not so whitish, crossveins usually closer together. Halteres yellow with brown stems. Genitalia fig. 2, b.

♀. Resembling male, abdomen with rather coarse hairs towards tip. Wings rather longer.

Length about 2 mm.

Both Mr. J. J. F. X. King and I caught this species in the neighbourhood of Orford (Suffolk) in June 1908, while in the same month and year Col. Yerbury took a pair at Gravesend (Kent). On 3rd July 1943 I caught a male in Woodditton Wood (Cambs.).

D. vagans Mg. This is the name under which the later described *xanthopygus* Strbl. must be known. The synonymy was admitted by Duda, though

he used Strobl's name for the species. It should be noted that the *Chlorops annulata* Mg. quoted by Duda was merely a change of name for the *Oscinis annulipes* Mcq., and that Macquart also described a *Chlorops annulipes* (a species of *CHLOROPINAE*) to which the reference given by Duda under *D.*

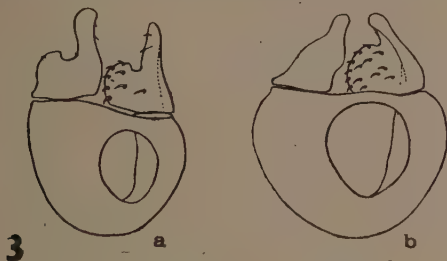


FIG. 3.—a. *D. vagans*, b. *D. styriacus*.

xanthopygus to a *Chlorops annulipes* Mg. applies. Male genitalia fig. 3, a. *D. vagans* Mg. is a comparatively common species in Britain.

Dicraeus vallis sp. n.

Belonging to the same group as *vagans*, *styriacus* and *napaeus*, but differing from *vagans* in its black pleurae and abdomen; from *styriacus* by its more yellowish front of frons, face, jowls and basal antennal joints, and blacker tarsi; and from the more closely allied *napaeus* as indicated in the description of that species.

♂. Front of frons, face, and jowls (except on occipital margin) yellow; jowls about as wide as third antennal joint, wider behind. Antennae with basal joints yellowish or brownish-yellow, third joint entirely brownish, sometimes with base beneath on inner side yellowish-brown. Palpi small, usually brownish-yellow. Pleurae black except for the vertical mesopleural suture, and mainly shining. Abdomen black, sometimes brownish about base, faintly dulled as usual by brownish dust, not shining on sixth tergite as in *styriacus*, and with rather large hypopygium (fig. 4, a) of which the lamellae are not so large or long as in *scibilis* and *fennicus*. Legs black, with only the knees narrowly yellowish and sometimes the extreme base of four anterior tarsi yellowish, otherwise tarsi black. Wings with costa rather noticeably thickened and dark as in *styriacus*. Halteres yellow.

♀. Closely resembling male except for pointed abdomen.

Length 2.2-2.5 mm.

At present known from the Devil's Ditch, near Newmarket (Cambs.), where it is not uncommon about the middle of June, and from Hogley, near Oxford, where Mr. A. H. Hamm has taken it.

Dicraeus napaeus sp. n.

Differing from *vallis* as follows:—Front of frons, face and jowls more brownish-yellow; jowls distinctly wider and their lower half browner and more punctate and striated; palpi brownish. Genitalia with side lamellae or claspers of different shape (fig. 4, b). Legs with tibiae narrowly yellowish at each end, and tarsi distinctly yellowish-brown, not black. Differing from *styriacus* by its wider facial orbits, and wider jowls.

Length 2.25 mm.

It will be noticed that while the legs are similar in colour to those of *styriacus* the head and antennae are not so dark as in that species, though.

darker than in *vallaris*, while the genitalia are different from either. Though at present known from only one male taken at Cornbury Park (Oxford) on

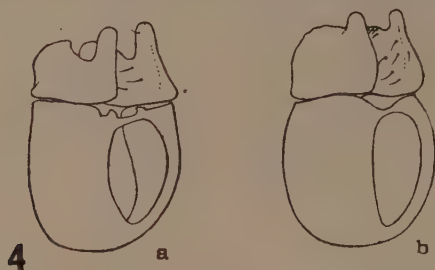


FIG. 4.—a. *D. vallaris*, b. *D. napaeus*.

4th July, 1904, it will certainly prove to be a distinct species in view of the fact that the equally closely allied *styriacus* and *vallaris* which have been taken in numbers have proved to be quite distinct.

D. styriacus Strbl. The British species to which I apply this name is very much like *D. napaeus*. Apart from the different male genitalia (fig. 3, b) and darker colour of head, the facial orbits (cheeks) are at their narrowest part only linear (in *napaeus* they are as wide as costa just beyond end of subcostal (r_1) vein) and the jowls below eyes at narrowest part are not wider than third antennal joint as they are in *napaeus*. The difference from *D. vallaris* in colour of head is very marked.

This species is not uncommon on the Devil's Ditch (Cambs.) at about the middle of June.

Mimogaurax Hall.

This name was proposed by Hall in 1937 in the place of *Pseudogaurax* Duda (1930) *nec* Malloch (1915). The single species *M. niger* Cz. is known as British only from the specimens bred by Mr. Basden from the nest of a Dormouse found at Bradfield (Berks) in June 1933.

Botanobia Lioy.

I dealt with the two British species in 1939 (*Ent. mon. Mag.* 75 : 151). *B. fascipes* Beck. has only one dark pleural spot (on mesopleura) and a narrow dark band at base of hind tibiae; in *B. dubia* Mcq. there are four dark patches on each pleura and the hind tibiae are entirely yellow.

Eribolus Becker.

Species of this genus have a distinctive flattened appearance coupled with a dusted, or partially dusted, frontal triangle, and the long axis of eye more diagonal. There are only a few (about four) orbital bristles and these are usually very uneven in length and one or two on each side may be much longer than the others. Duda placed such great faith in the dusted or polished frontal triangle as generic characters that he did not include *Oscinella gracilior* Meij. (known to him by description only) in *Eribolus* but in *Oscinella*, in spite of de Meijere's description of "Thorax ziemlich flach." The species I have recognised as *gracilior* while having the frontal triangle polished except for a

square area including the ocelli, and the extreme sidemargins towards apex, possesses the distinctive appearance of a species of *Eribolus*, and is certainly more correctly placed therein.

- 1(6). Frontal triangle entirely obscured by dust.
- 2(3). Front of frons narrowly but distinctly reddish-yellow. Triangle large, extending almost to front of frons. Jowls almost as wide in front as third antennal joint, the latter and palpi black *nana* Zett.
- 3(2). Frons all dark. Triangle shorter. Antennae at least yellowish beneath or jowls much narrower.
- 4(5). Third antennal joint smaller and only pale at extreme base beneath (♂♀). Palpi darker. Jowls narrower in front. Tibiae more obviously ringed *hungaricus* Beck.
- 5(4). Third antennal joint larger and paler beneath in ♂, only basal joints and extreme base of third joint beneath pale in ♀. Palpi yellow in male, brown in female. Jowls in front quite half width of third antennal joint. Anterior tibiae yellow in male or only obscurely ringed in female *slesvicensis* Beck.
- 6(1). Frontal triangle polished except for area about ocelli. Front tibiae mainly and all tarsi pale yellow, other tibiae pale at both ends . . . *gracilior* Meij.

E. nana Zett. Duda does not accept the synonymy of this species with *E. sudeticus* Beck. Unfortunately Zetterstedt does not mention the colour of palpi in *nana*. Becker gives *nana* as having yellow palpi, but his description of the colour of legs does not agree with Zetterstedt's description; this latter, however, does agree with *sudeticus* Beck. I consider that Becker's *nana* must have been a different species, and not Zetterstedt's *nana*. I have seen this species from only Herefordshire (Cliffords Castle and Moccas Park).

E. hungaricus Beck. I have taken this species on the coast of Essex, Suffolk and Dorset, and in Chippenham Fen (Cams.).

E. slesvicensis Beck. Also not uncommon on the Essex and Suffolk coasts.

E. gracilior Meij. I have taken only three males of this species, two at Barton Mills (Suffolk) in May, and one at Holywell Row (Suffolk) in June. Since the above was written three further males have been taken, in the dried-up garden pond here at Newmarket. Mesnil's *O. gracilior* (1936, *Ins. nuisibles aux plantes cultivées* 2) is not Meijere's species but is my *Oscinella trochanterata* (see below).

Tropidoscinis Enderlein.

This genus, founded upon a Brazilian species, was adopted by Duda for two new European species *zurcheri* and *gallarum* which had the frontal triangle dusted but less densely so than in *Conioscinella*; under this latter genus he stated that *zurcheri* was more typical of *Tropidoscinis* and *gallarum* somewhat intermediate between the two genera. *T. zurcheri* has the shape of head of *Oscinella* and the same number (about 4) of distinct orbital bristles while the head and greater number of orbital bristles of *gallarum* makes it necessary in my opinion to place that species in *Conioscinella*. This is further emphasised by the similarity in arrangement of the thoracic microchaetae in *zurcheri* and *Oscinella*, and *gallarum* and *Conioscinella*, respectively. Therefore species truly congeneric with *zurcheri* are those agreeing with *Oscinella* except for a dusted frontal triangle, and if this be accepted certain species placed by Duda in *Conioscinella* must be transferred to *Tropidoscinis*. This applies to the British species *albipalpis* Mg., *kerteszi* Beck., and *nigrifrons* Duda. In *Tropi-*

doscinis the front margin of frons is rather more produced than in *Oscinella* and is convex when viewed from above, whereas in *Oscinella* it is concave.

- 1 (6). Front of frons, and jowls below eyes, yellow.
- 2 (3). Front of frons broadly (almost half its length) yellow; jowls wider, distinctly wider than front tibia and pale yellow; palpi usually yellow *albipalpis* Mg.
- 3 (2). Front of frons only narrowly yellow; jowls narrower, scarcely so wide as front tibia, and obscurely yellowish, or darkened on lower margins.
- 4 (5). Antennae partly yellow; palpi yellow; four anterior tibiae and all tarsi mainly yellow *antennata* sp. n.
- 5 (4). Antennae and palpi black; legs much darker *kerteszi* Beck.
- 6 (1). Frons and jowls entirely dark.
- 7 (10). Frontal triangle extending to front of frons; subapical wing cell widening out at tip.
- 8 (9). Both ends of four anterior tibiae and first 2-3 joints of middle tarsi conspicuously yellow. Orbital bristles longer *zurcheri* Duda.
- 9 (8). Legs black with only base of front tibiae obscurely yellowish. Orbital bristles shorter *scotica* sp. n.
- 10 (7). Frontal triangle not extending to front of frons; subapical cell not widening out towards tip. *nigrifrons* Duda.

T. albipalpis Mg. is a very distinct species with its deep black antennae in strong contrast to the yellow front of head. It was confirmed as a British species of *Oscinis* in 1911. It occurs both on the sea-coast and inland.

***Tropidoscinis antennata* sp. n.**

♂. The only species of *Tropidoscinis* with partly yellow antennae.

Head similar in shape to that of *zurcheri*. Front of frons narrowly yellow, rest of frons dull blackish, except on the large frontal triangle, which is more shining (though slightly dulled by microscopic pile); this triangle, which almost exactly resembles in texture and appearance the disc of thorax, is not full width of frons behind and extends forward rather more than half length of frons (not quite to limit of darkened part). Face whitish-yellow, the very narrow jowls of similar colour next to eye but dark on and below the single row of small dark buccal hairs, below these hairs on posterior half of mouth margin there are a few pale hairs. Clypeus and proboscis black. Palpi yellow. Frontal bristles all shorter than in *zurcheri*, dark. Inner vertical bristle decidedly shorter than outer, about length of ocellar and orbital bristles. Antennae yellow, but third joint darkened above, more extensively so on outer than on inner side. Arista and eyes microscopically pubescent, the pubescence on former shorter than in *zurcheri*, on latter rather less dense.

Thorax and abdomen shining black all somewhat dulled by microscopic greyish-brown pile, except greater part of pleurae (to same extent as in *zurcheri*) which is not dusted. Thoracic microchaetae rather sparse and arranged more or less in lines as in *zurcheri* but shorter. All thoracic and abdominal bristles and hairs dark.

Legs with femora black except at extreme tip, hind tibiae with a broad blackish band leaving base and tip yellow; four anterior tibiae and all tarsi except last 2-3 joints yellow, these latter becoming successively browner until last joint is dark brown, the tibiae sometimes with a brownish ring.

Wings slightly brownish below costa and about base, rather long and narrow, length measured from the pair of small costal bristles near base compared with width opposite outer crossvein as 50:21. Position of middle crossvein from base compared with distance from tip of wing as 18:32; this crossvein opposite end of subcostal vein (R^1), and well

beyond middle of cell below it. Subapical cell somewhat dilated at end owing to curvature upwards of end of cubital vein. Postical vein not extended to wing margin. Squamae small and dusky. Halteres pale yellow.

♀. Similar to male in all respects except that the abdomen ends in a pair of slender, dark, hairy papillae.

Length 1-1.25 mm.

Described from six males and three females taken in my garden at Newmarket (Suffolk) in July, all except one of them in a dried-up artificial pond into which, many years ago, sedge and other plants from Wicken Fen were introduced.

T. kerteszi Beck. has front of frons narrowly pale, varying from yellow to yellowish-brown, jowls also obscurely yellowish. Third antennal joint large and intensely black; arista almost thickened with pubescence. It is not uncommon in Chippenham Fen (Cambs.) in June, and I have found it in Suffolk in July and in Oxfordshire in August.

T. zurcheri Duda occurs where reeds flourish. I have bred it from the galls of both *Lipara lucens* and *similis* and taken it in Cambs. and Berks, and Col. Yerbury found it in Devon. It is somewhat like *Oscinella angustipennis* Duda, but of course the frontal triangle is somewhat obscured by dust. The four anterior tibiae are distinctly yellowish at both ends.

Tropidoseinis scotica sp. n.

Primarily distinguished from other species with a black head by its very black legs.

♀. Head not so intensely black as in *zurcheri*, more brownish-black. Ocellar or frontal triangle large, practically as wide as frons behind, and extending to (or almost to) front of frons. Frontal bristles short as in *antennata*. Occiput rather more convex than in either that species or *zurcheri*. Jowls narrow. Third antennal joint rather larger than in *antennata*, black; arista with similar short pubescence. Eyes very indistinctly pubescent. Palpi black.

Thorax and abdomen as described for *antennata* but abdomen has a tendency to be chestnut-brown in colour and its pubescence of a brownish tinge.

Legs black with only the knee joint on four anterior legs very narrowly and rather obscurely yellowish. Four posterior tarsi also with a tendency to reddish-brown.

Wings rather similar in shape and coloration to those of *antennata*, the corresponding measurements being as 55 : 22 and as 19 : 35. The subapical cell is more gradually widened towards tip.

Length about 1.25 mm.

Described from a female taken by Dr. C. G. Lamb at Nethy Bridge (Inverness) in June 1905, and another female taken by myself at Kinrara, near Aviemore, in the same county, in June 1937. The jowls are about as wide as front tarsi.

T. nigrifrons Duda. This species is not unlike *kerteszi* except that the frons is entirely dark, antennae not so large or intensely black and arista not so pubescent. Palpi dark. Legs black with knees (especially on four anterior legs), base and tip of tibiae (especially of same legs) yellowish, and four posterior tarsi brownish-yellow except towards tip. Smaller or larger patches on frontal triangle each side of ocelli may be bare (noted in Duda's Errata), in one British pair so large that the specimens might be passed as a species of *Oscinella* if the more projecting and convex front margin of frons is overlooked. I have taken *T. nigrifrons* in Suffolk, and Col. Yerbury took it in Essex, Dorset, and Glamorgan.

- 20(21). Legs entirely black (usually including tarsi) and rather stouter, especially noticeable on tarsi. Arista rather more distinctly pubescent *nigerrima* Mcq.
 21(20). Legs rarely entirely black, more slender especially on tarsi (fig. 6, a), which are yellowish about base. Arista not so distinctly pubescent
frit L.

O. albiseta Mg. Duda incorrectly uses the name *maura* Fln. for this species. There can be no doubt from statements made by Zetterstedt that Fallen included both *albiseta* and another species much more allied to *frit* under his *O. maura*, but Meigen by describing the species with thickened whitish arista as *albiseta* limited the name *maura* Fln. to the *frit*-like species, and in this he was correctly followed by Zetterstedt and others. Mesnil has bred *albiseta* (called by him *maura*) from grasses of the genus *Dactylis*.

O. angustipennis Duda. This species is easily recognised by its very long, narrow, brownish, wings. The frontal triangle almost reaches front of frons, jowls below eyes are narrow, being about as wide as tip of front tibia, fourth joint of male middle tarsi short and almost globular. I have taken it in Cambs. (Whittlesford and Snailwell) and Suffolk (Barton Mills), and Col. Yerbury took it in Glamorgan (Porthcawl), all in the month of June.

O. posticata Coll. When describing this species I compared it with *O. trigonella* Duda, the name under which I then thought our British *O. nitidissima* Mg. would have to be known. However, in the meantime it has been proved, as stated under the next species, that the name *nitidissima* Mg. has been correctly used by British Dipterists for a species allied to *frit*, so that instead of "*trigonella* Duda" in my description one should read "*nitidissima* Mg." In spite of the agreement in many respects of Duda's description of *trigonella* with my *posticata*, it is impossible to reconcile his description of the male genitalia with the figure here given of *posticata* genitalia, Duda's description being as follows: "Genitalien anders als bei *frit* gebildet. Hintere Genitalanhänge des ♂ basal borstig behaart, jederseits mit einem stark sichelförmig nach vorn gekrümmten, kahlen und spitzen hinteren Haken und einem auf der konvexen Seite dicht abstehend behaarten, nach hinten gekrümmten stumpf endenden plumperen vorderen Haken endend." The nearest approach to genitalia of this description known to me are those of the



5
 FIG. 5.—*O. posticata*.

next species. In *O. posticata* genitalia (fig. 5) the two very small, triangular, and bare "Haken" near the anus are distinctive for the species; in other British species they are larger and of different shape.

O. nitidissima Mg. Duda considered that Meigen's description of "Stirne . . . fein punktirt" indicated a species of *Goniopsita*, but Sabrosky, who has seen the type in Meigen's Collection, stated in 1939 (*Ann. ent. Soc. Amer.*

32:323) that it is "the well-known, polished variety of *frit*." It is probable that Meigen's "fein punktirt" was merely in contrast to the "hohlpunktig" frons of his previous species *atra* which is recognised as a species of *Goniopsita*. Duda appears to have described *nitidissima* as *frit* var. *atricilla* Zett. We appear to have two forms of this species in Britain, one (typical) with paler legs (the four anterior tibiae almost yellow) and jowls rather narrower and entirely dull, the other with darker legs and slightly wider, more shining, jowls.

***Oscinella trochanterata* sp. n.**

♂♀. Resembling *pusilla* in having front and middle tibiae entirely yellow, but front trochanters, and tip of all femora (broadly) yellow; frontal triangle not extended to front of frons, and tarsi stouter, especially towards tip.



FIG. 6.—Mid tarsus of: a, *O. frit*, b, *O. trochanterata*.

♂. Compared with *pusilla*:—Frontal triangle only $\frac{2}{3}$ to $\frac{3}{4}$ length of frons, the dull frontalia therefore larger; face in profile rather more retreating, the head being longer above. Third antennal joint larger, arista more distinctly pubescent. Jowls though deep not so deep as third antennal joint.

Thorax more densely dusted or microscopically pilose on disc, and the dust greyer, giving thorax a duller grey appearance. Abdomen narrower and more densely dusted, pubescence paler, basal segments seldom pale.

Legs with conspicuously yellow front trochanters, others tawny; all femora more broadly yellow at tip, base and tip of hind tibiae yellow; tarsi yellow or brownish-yellow, always paler about base, especially on middle tarsi, all rather longer and more pubescent, and certainly stouter towards tip; on middle tarsi last joint as long as second (longer than third), fourth joint short and deeply excised on upper apical margin (fig. 6, b).

Wings rather longer, slightly yellowish-brown. Squamae pale yellow. Halteres yellow to base, stem only richer yellow than knob.

♀. Resembling male but often larger. Abdomen pointed behind, the telescopic ovipositor of a tawny colour, terminal papillae long and slender. Middle tarsi more normal but last joint longer than third.

Length varying from 2 to nearly 3 mm., the female usually the larger.

This species occurs commonly on *Phalaris arundinacea* growing in a damp, though no longer water-filled, artificial pond in my garden at Newmarket (Suffolk), and Mr. F. D. Goodliffe of the Lord Wandsworth College of Long Sutton, Hants, has bred it from that plant. I had previously recognised the species from specimens taken by Col. Yerbury at Porthcawl (Glamorgan) in July 1906 and by myself at Barton Mills (Suffolk) and Tram Inn (Herefordshire). It is the *Oscinella gracilior* of Mesnil (1936) *nec* Meijere (1918) which is an *Eribolus*.

Oscinella angularis sp. n.

♂♀. Obviously related to *trochanterata*, having shining part of frontal triangle not extended to front of frons, and similar male middle tarsi, but distinguishable at once by colour of legs.

♂. Compared with *trochanterata* :—frons in profile rather shorter and occiput at level of lower margin of eye not so broad; frontal triangle (or at least shining part of same) smaller because dusted at angles; jowls slightly narrower; arista with rather shorter pubescence. Lamellar appendages of genitalia of different shape. Legs much darker, front trochanters dark, four anterior knees and tips of tibiae only narrowly pale, hind knees at most only reddish-brown; front tarsi usually darkened, four posterior tarsi yellow on two basal joints. Wings a little shorter. Stems of halteres darkened.

♀. As usual rather larger than male, but otherwise similar except for more normal fourth joint to middle tarsi, and pointed end to abdomen.

Length 1.5–2 mm.

This species occurs with *O. trochanterata*, but much more sparingly, in the artificial pond at Newmarket (Suffolk), and I have also taken it near Mildenhall (Suffolk). Mr. F. D. Goodliffe has bred it from *Phalaris arundinacea* in Hampshire. The pupae of this species appear to be recognisably distinct owing to their more prominent transverse corrugations.

Oscinella cariciphila sp. n.

♂♀. A species resembling *pusilla* in having front and middle tibiae practically entirely yellow, but jowls very narrow, and arista more distinctly pubescent.

♂. Shining frontal triangle extended to front of frons; third antennal joint about as in *frit*, slightly larger than in *pusilla*; arista with longer pubescence than in either. Jowls very narrow, not wider at narrowest part than tip of front tibia.

Thorax a little more finely punctate and less dusted than in *pusilla*. Abdomen only slightly reddish about base; side lamellae or paralobes of genitalia not so wide as in *pusilla*. Legs with front and middle femora only very narrowly yellow at tip, and their tibiae usually entirely yellow, rarely a faint darkening about middle of front tibiae; hind tibiae only narrowly and often obscurely yellow about base and tip; four posterior tarsi pale about base. Middle tarsi of normal narrow build, last joint not enlarged and (without ungues) scarcely so long as third joint, end margin of fourth joint not excavated above nor produced beneath, and almost as long as fifth.

Wings rather short, broad, and blunt-ended, slightly brownish. Halteres with brownish stems.

Length about 1.25 mm. (♂), to 2 mm. (♀).

This species first became known to me from a long series of specimens taken on a patch of *Carex* growing in a damp spot near where the railway crosses the stream at Kennett (Cambs.) on 27th June 1942. There it appeared to be the

only species present. I have taken it elsewhere in Cambs., and in the old artificial pond in my garden at Newmarket (Suffolk), always in association with *Carex*. It has the narrowest jowls of any of the *frit* group of species.

O. vastator Curt. This is a species originally described from specimens bred from young wheat plants, and is at present not well known to me owing to lack of material. It almost certainly (as in the case of *O. frit*) also attacks some grasses because specimens in my collection were taken in the paddock behind my house late in May and in June 1894 far away from wheatfields, but searching the same locality in recent years has failed to produce more specimens. Its wider jowls, middle tibiae distinctly yellow at base as well as tip, and wider paralobes to male genitalia help to distinguish it from *frit* and allied species. It is probably more nearly related to the next species but among other distinctions the hind tibiae are never so distinctly yellow at base and tip as in *pusilla*.

O. pusilla Mg. According to Meigen's description, this species should have all tibiae and tarsi pale, but Becker, who had seen the type, used the name for specimens with middle of hind tibiae darkened, and there is no known European species answering to Meigen's description, therefore I follow Becker in the use of the name. The references to *O. pusilla* given by Duda (1933) under the names of Giraud, Cohn, Perris, Kaltenbach, Brauer, and W. Hugo (a mistake for Hugo Wilhelm), are incorrect. Giraud's species was bred from *Lipara* galls on *Phragmites* and was probably *Calamoncosis minima* Strbl. The black-legged species bred by Cohn and H. Wilhelm from young oat plants was *O. frit* L. Kaltenbach referred to Cohn's species and Brauer to Giraud's, while Perris' species (bred from dead branches of "Pin maritime") was certainly not an *Oscinella* as proved by the description. The breeding of *O. pusilla* from barley grains and field specimens of *Hordeum murinum* has been recorded by Cunliffe (1921), and I use the name for this species associated with *Hordeum*, but (as in the case of *vastator*) much more material is needed to fix the limits of the species. *O. grossa* Mesnil, bred from *Aira* and barley in France, must be closely allied, if not the same species.

Oscinella hortensis sp. n.

♂♀. In colour of legs and width of jowls intermediate between *cariciphila* and *pusilla* but certainly distinct.

♂. Shining frontal triangle almost extended to front of frons. Third antennal joint small as in *pusilla* but jowls narrower though not so narrow as in *cariciphila*, not so wide as third antennal joint. Aristal pubescence shorter than in this latter species. Thorax more finely punctate and less dusted than in *pusilla*; the curved paralobes of genitalia narrower than in that species. Legs with four anterior tibiae with an ill-defined (and rather variable in extent) dark ring about middle, their femora only very narrowly yellow at tip; hind legs darker, their tibiae only narrowly yellow at tip, and often only narrowly reddish-brown at base; four posterior tarsi yellow on at least first two joints, but front tarsi at most only yellowish about base of first joint. Middle tarsi narrow and normal but rather shorter than in either *cariciphila* or *pusilla*. Wings rather short and broad, faintly brownish. Stems of halteres darkened.

♀. Differing in having legs always more extensively pale, middle tibiae often entirely yellow, hind tibiae more distinctly yellow at both ends; middle tarsi as in male. Stem of halteres often not darkened. Primarily differing from *pusilla* ♀ in its narrower jowls and more finely punctate thorax.

Length 1.0–1.5 mm.

This is probably a common and widespread species. It first became well known to me from a long series taken on my garden lawn here at Newmarket (Suffolk) on 29th June 1942, where it was almost the only species present. The sexual difference in colour of legs may well have been partly responsible for the belief that this character was of no value for distinguishing species in the genus. There may be some difficulty in separating dark males of this species from immature males of *frit*, but the latter in addition to longer and clearer wings have the vibrissal angle of face more prominent in profile, the width of jowls from angle to eye margin being much greater than it is opposite posterior eye margin.

O. nigerrima Mcq. This almost entirely black-legged species needs comparison only with black-legged specimens of *frit*. It is usually larger with stouter legs and brownish wings. Third antennal joint rather larger and arista more distinctly pubescent. Eyes with longer hairs. Palpi stouter. Thorax more dusted and duller. Legs black with, at most, only middle and hind tarsi brownish about base, tarsi particularly not so slender.

This is the first species of the genus to appear in the spring and is probably common. I have taken it at Barton Mills and Newmarket (Suffolk) and Chippenham Fen (Cambs.) on grass in April and May. Specimens also occur again in July, so that the species is apparently at least double-brooded, and as such specimens are in all respects similar to the spring ones, the dark legs of the spring brood are not a seasonal variation. As Macquart's description of *nigerrima* is applicable to this species I make use of it instead of describing the species as new.

O. frit L. When describing this species in 1750 as *Musca frit*, Linné stated that the larvae caused serious damage to barley in Sweden by attacking the immature grains, causing them to become shrivelled and worthless. He repeated this in 1758, 1761 and 1767, and described the species as black with halteres and soles of hind feet pale, abdomen "fuscum, subtus magis pallide virens." No species answering to this description attacks barley grains in this country, where the only *Oscinella* very rarely bred from barley grains is *O. pusilla* Mg.

In 1781 Bjerkander described a *Musca avenae* injurious to oats in Sweden, the fly being entirely black with brownish eyes. The attack on the oat plant by the larvae was described in the German edition (1784) of Bjerkander's paper as follows: "Wenn der Haber anfängt Halme zu bekommen, fangen die Maden an, sie abzuschneiden, erst am untersten Gliede dann an den übrigen. Nur der letzte Schaden, die sie thun, wird dem Landmanne merklich, weil die *paniculae* vertrocknen und weiss werden." Though Bjerkander considered the fly to be somewhat like *M. frit* L., he thought it improbable that one species could be responsible for such very different damage. *M. avenae* Bjerk. is, however, now considered to be a synonym of *M. frit* L.

In Britain by far the greatest damage to any cereal crop by species of *Oscinella* is that to oats by larvae attacking the young plants in the spring and (later) the ripening grain. Unless oats are attacked by more than one species of *Oscinella* (which is by no means impossible), our species, which answers to Curtis' description of *O. granarius*, is the *M. avenae* of Bjerkander. The probability that it is also *M. frit* L. rests on the fact that Haliday stated in 1851 that the three specimens of *M. frit* in the Linnaean Collection in London were representatives of *O. granarius* and *vastator* Curt. I therefore accept the *Oscinella* bred from oat grains as typical *O. frit* L. This species normally has the extreme base and tip of front tibiae, at least the tip of middle tibiae, and

all tarsi about base, pale; the pale parts of, at least, tibiae being more yellowish-brown than yellow. It should be noted, however, that Westwood recorded as *M. avenae* Bjerk. specimens with entirely black legs bred from oat grains, and similar specimens occur in the spring which are not easily distinguished from *O. nigerrima*.

I have seen specimens, apparently identical with those bred from oats, reared by Mr. F. D. Goodliffe from young barley plants and from maize, while Cunliffe (1921) reported the infection in August of certain grasses by flies bred from oat grains, and the emergence in the following spring of flies from the infected grasses; unfortunately he did not state whether these latter specimens agreed with their parents in colour of legs. Thus, in spite of the uncertainty in the identity of the insects in records of the breeding of what has been called *O. frit*, it would appear proved that this species at least is not confined to one host plant.

In July 1922 I swept from the garden lawn of Sussex Lodge, Newmarket (Suffolk), a number of a very small form of *O. frit* easily distinguishable from typical *frit* obtainable in that month of the year in fields of spring oats. It is possible that this is the true *O. atricilla* of Zetterstedt which he considered might be only a variety of *frit*. Some day it may be possible to examine the types of this and other species in the light of our increased knowledge and clear up the synonymy, in the meanwhile to avoid adding to the confusion in the use of the name *atricilla* I describe my variety as:—

***Oscinella frit* var. *exigua* var. n.**

Smaller than typical *frit*. Thoracic disc with dusting (or microscopic brownish pile) rather more distinct, but *puncturation* finer and consequently thorax rather more *shining*-black. Legs black with tarsi to a large extent yellowish from base onwards, but tip of middle tibiae not distinctly yellowish. Wings shorter and broader with crossveins rather closer together and discal vein with a greater tendency to be slightly downcurved at tip.

Length about 0.75 mm. ♂ to 1.25 mm. ♀.

The *O. hortensis* taken on the neighbouring garden lawn of "Raylands" is so different in size and colour of legs that it cannot be confused with the above. They certainly must have a different life-history.

***Lioscinella* Duda.**

This generic name was first proposed by Duda for a subgenus of *Oscinella* Beck. in 1929 (*Konowia* 8 : 168) in the following words : " Das Subg. *Lioscinella* begreift die *Oscinella*-Arten Beckers bei denen das Stirndreieck kahl, glatt und glänzend und der Thorax wenigstens im Bereiche des Mesonotums überwiegend kahl besw. unbereift ist." In 1932 Duda discontinued the use of the name, but I retain it for the *anthracina* group of Becker's *Oscinella*, for which it was apparently originally intended, and which can be recognisably distinguished from *Oscinella*.

The British species of this genus may be tabulated as follows :—

- 1(4). Legs entirely yellow.
- 2(3). Jowls below eyes linear (not so wide as palpi); eyes larger and rather more reniform; frontal triangle extending practically to front of frons; antennae smaller; arista with longer pubescence . . . *anthracina* Mg.
- 3(2). Jowls wider; eyes smaller and more oval; frontal triangle about $\frac{2}{3}$ length of frons; frontal bristles longer; antennae larger; arista with shorter pubescence . . . *atricornis* Ztt.

- 4(1). Legs partly or wholly darkened.
 5(8). Legs only partly darkened. Thoracic disc not dusted behind except in scutellar suture.
 6(7). Usually only middle femora with a dark ring or band, hind tibiae clear yellow; humeri and notopleural area dusted; jowls wider . . . *fasciola* Mg.
 7(6). All femora, or at least four posterior, partly darkened, and hind tibiae brownish about middle; humeri and front part of notopleural area shining; jowls linear *femoralis* sp. n.
 8(5). Legs entirely darkened. Thoracic disc extensively dusted behind, and especially at sides. Species with smaller eyes and wider jowls of *atricornis*, but smaller antennae and pubescent arista of *anthracina*; frontal triangle about $\frac{2}{3}$ — $\frac{3}{4}$ length of frons *atripes* Duda.

L. anthracina Mg. is a common species in southern England. I can record its occurrence in Cambs., Suffolk, Norfolk and Glamorgan.

L. atricornis Zett. and *atripes* Duda are known to me only from the Spey Valley (Inverness-shire).

L. fasciola Mg. The sides of thoracic disc (including whole of notopleural depression), and humeri, are dusted as in *atricornis*, but the jowls are rather narrower without being as linear as in *anthracina*. Though the eyes are larger and arista pubescent as in *anthracina*, the frontal triangle is not so large as in that species. There may be some slight darkening on hind femora but the dusted humeri and notopleural depression distinguish it from *femoralis*.

Becker, who had seen the types of both *fasciola* Mg. and *fascipes* Mg., placed them as synonyms of *anthracina* Mg.; they must therefore be species of *Lioscinella*. He did not accept the leg coloration as of specific value and overlooked the other distinctive characters. There are certainly two distinct species in Britain with dark markings on the femora, and one of these (known to me at present from two males taken in Cambs. and one in Norfolk) answers sufficiently well to the description of either of Meigen's species to make it advisable to use for it the name *fasciola* and consider *fascipes* a synonym.

The second British species, though obviously included by Duda under his var. *fasciola* of *anthracina*, is here described as :—

Lioscinella femoralis sp. n. ♂♀.

Head somewhat resembling that of *anthracina* Mg., having similar almost linear jowls, but frontal triangle not so long— $\frac{2}{3}$ — $\frac{3}{4}$ length of frons. Thorax with humeri and greater part of notopleural depression quite devoid of dust. Legs with front femora often only faintly, but other femora very distinctly, darkened; hind tibiae also brownish about middle; tarsi as usual brownish towards tip. Wings faintly brownish. Squamae and halteres yellow.

Length scarcely 2 mm.

This species is not uncommon in Chippenham Fen (Cambs.), and has also occurred in the disused artificial pond at Sussex Lodge, Newmarket (Suffolk).

Hapleginella Duda.

H. laevifrons Lw. is a very distinct shining black species with partly yellow antennae and legs and dense, scattered, hairs on thorax. It is widely distributed and I have taken it in some numbers by beating conifers. My specimens are from Nairn, Inverness, Cambs., Suffolk and Hants.

Elachiptera Macquart.

Duda (1932) included the next two genera under the name *Elachiptera*, and did not accept any of the other generic subdivisions. I differ from him only in retaining *Melanochaeta* and *Gampsocera* as distinct on characters not hitherto employed. The British species of *Elachiptera* may be distinguished as follows :—

- 1 (6). Thorax yellow, or partly yellow, at least with distinctly yellow humeri.
- 2 (3). Wings very much abbreviated, much shorter than abdomen
brevipennis Mg.
- 3 (2). Wings of normal length.
- 4 (5). Only one pair of orbital bristles. Thorax yellow with two dark supra-
alar patches, and pleurae partly black *uniseta* Coll.
- 5 (4). Two pairs of orbital bristles as usual. Thorax black with yellow
humeri, postalar calli, and greater part of meso- and ptero-pleurae
megaspis Lw.
- 6 (1). Thorax black without distinct yellow patches.
- 7(16). Disc of scutellum strongly punctate or roughened. Marginal scutellar
bristles arising from distinct, though sometimes small tubercles.
- 8(13). Disc of thorax not universally dusted, shining and without dust on
three (or at least two) longitudinal stripes.
- 9(10). Frontal triangle yellow. Thorax dusted with a narrow shining
stripe on each side only *rufifrons* Duda.
- 10 (9). Frontal triangle black. Thorax extensively shining on median and side
stripes.
- 11(12). Wings longer. Apical scutellar bristles closer together, very little
wider apart than they are from each lateral bristle. Abdominal hairs
pale yellow. *cornuta* Flin.
- 12(11). Wings shorter. Apical scutellar bristles nearly twice as far apart as
they are from each lateral bristle. Abdominal hairs darker
diastema sp. n.
- 13 (8). Disc of thorax universally even if only thinly dusted, or shining on
front margin only.
- 14(15). Scutellum longer than broad with 4-6 very distinct marginal tubercles.
Legs pale yellow *tuberculifera* Corti.
- 15(14). Scutellum not longer than broad with quite small tubercles. Legs with
at least femora tawny brown *scrobiculata* Strbl.
- 16 (7). Disc of scutellum smooth, not punctate or rugose, the short lateral and
longer apical bristles not arising from tubercles. Thorax con-
spicuously dusted. Palpi projecting well beyond epistoma
pubescens Thalh.

E. brevipennis Mg. is common throughout the winter under heaps of cut litter or sedge in marshy places.

E. uniseta Coll. was described in 1939 (*Ent. mon. Mag.* 75 : 150). I have seen no additional specimens.

E. megaspis Lw. In this species the first three abdominal tergites are fused together, and the venter pale yellow with very narrow sternites. It is not uncommon, at any rate in the southern half of England where watercress (*Nasturtium officinale*) grows, in May and again in the autumn.

E. rufifrons Duda (described as a variety of *cornuta*). I use Duda's name for a species resembling *cornuta* but with an entirely yellowish frontal triangle, and thoracic disc much more extensively dusted, in spite of the fact that he does not mention this second very striking character. The frontal triangle is slightly smaller than in *cornuta* and the posterior angles (to a point just beyond

front ocellus) are conspicuously dusted, so that the shining front part of frontal triangle is smaller and narrower than in *cornuta*. The whole of thoracic disc except for a narrow stripe on each side from inner corner of humerus to postalar callus is dusted greyish. The dusted area on upper hind corner of mesopleura and upper part of pteropleura is also more extensive.

I captured a male at Oare (Kent) on 3rd August, 1937, and a female at Upton (Norfolk) on 21st June, 1928. I have seen a second male taken by Dr. F. W. Edwards at Beaulieu Road (Hants) on 2nd September, 1925.

E. cornuta Fln. is very common everywhere.

Elachiptera diastema sp. n.

♂♀. Resembling *cornuta* but having shorter wings, apical scutellar bristles wider apart, and abdominal pubescence darker.

A rather broader insect than *cornuta*. The shining black frontal triangle rather broader and longer; hairs and bristles on head darker, especially the peristomal hairs. Thorax with similar puncturation and dusted stripes, but these stripes joined behind by a prescutellar dusted band, absent in *cornuta*; scutellum shorter and rather more truncate at tip with a much greater distance between apical bristles than between either and the nearest lateral bristle. In *cornuta* the apical bristles are decidedly nearer together. Abdomen rather broader with pubescence shorter and not so pale. Legs with a decided tendency to be darker on an apical band on hind femora, and a smaller patch or band on four anterior femora; front tarsi and end of front tibiae brownish-black.

Length about 2 mm.

Probably an overlooked species. I have taken it in March and April at Barton Mills (Suffolk) and Chippenham Fen (Cambs.), and have seen it from Oxford (taken in March), and from Dorset (in August and September).

E. cornuta may sometimes develop the femoral darkening of *diastema*, but is always easily distinguished by its longer wings, disposition of scutellar bristles, and longer and paler abdominal pubescence. It is impossible to associate this new species with certainty with any of the described varieties or synonyms of *cornuta*.

E. tuberculifera Corti can be recorded from Devon, Sussex, Oxford and Cambs. It is a common species in Woodditton Wood (Cambs.) in May.

E. scrobiculata Strbl. occurs in the same situations as *brevipennis*. It is common in Chippenham Fen (Cambs.).

E. pubescens Thalh. appears to be confined to coastal districts in the south of England. I caught a number of specimens at Abbotsbury (Dorset) in May 1937, and Col. Yerbury had previously taken it at Studland (Dorset) and Christchurch (Hants).

Melanochaeta Bezzi.

M. capreolus Hal., except for its arista, might easily pass as a species of *Oscinella*.

Melanochaeta is obviously a connecting link between *Oscinella* and *Elachiptera*. I have taken the species in three different localities in Cambridgeshire in May and June.

Gampsocera Schiner.

G. inornata Corti is at present known as British from the single female taken by Mr. H. Britten at Mulgrave Wood, Yorkshire, on 11th November, 1905. Duda considers it to be only a variety (without the usual wing markings)

of *numerata* Heeg., but in the Yorkshire specimen, at least, there is a further important difference in the position of the middle (cubito-discal) crossvein of wings; this is some distance before the end of subcostal vein; in Duda's figure of the wing of *numerata* this crossvein is practically opposite end of subcostal vein.

INDEX TO GENERA.

	PAGE		PAGE
Aphanotrigonum	125	Lipara	119
Botanobia	134	Melanochaeta	147
Calamoncosis	120	Mimogaurax	134
Conioscinella	128	Oscinella	138
Dicraeus	130	Oscinimorpha	124
Elachiptera	146	Oscinisoma	128
Eribolus	134	Polyodaspis	121
Gampsocera	147	Siphonella	121
Goniopsita	122	Siphunculina	123
Hapleginella	145	Trachysiphonella	123
Lasiambia	123	Tricimba	129
Lioscinella	144	Tropidoscinis	135

Vol. 97. Part 6. Pp. 149-176, 68 figs.

25th September, 1946.

THE

IMP. INST.
— LIBRARY

TRANSACTIONS

30 SEP 1946

OF THE

SERIAL

Eu. 344

ROYAL

SEPARATE

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

	PAGE
X ZAKHVATKIN, A. A., D.Sc. Studies on the Homoptera of Turkey	149-176, 68 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D. }

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS G. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBS, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. **British National Committee for Biology** (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. **Local Committee of Management of Wicken Fen.**

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. **National Trust for Places of Historic Interest or Natural Beauty.**

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. **New Forest Association.**

Mr. W. Fassnidge, appointed 1934.

5. **New Forest Joint Committee.**

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. **Royal Meteorological Society. Phenological Committee.**

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. **Biology War Committee.**

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. **Council for the Promotion of Field Studies.**

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. **Joint Bioclimatic Committee.**

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

STUDIES ON THE HOMOPTERA OF TURKEY. I-VII

By A. A. ZAKHVATKIN, D.Sc.

(Zoological Institute, University of Moscow.)

(Communicated by the Honorary Secretary.)

Manuscript received 14th February, 1945.

(Read 5th June, 1946.)

WITH SIXTY-EIGHT TEXT-FIGURES.

MANY years ago I received for identification from the British Museum (Natural History) a considerable number of Auchenorrhynchous Homoptera, taken by Dr. B. P. Uvarov during his journey to Asia Minor in 1931. Some time later, Mr. N. N. Jenjouriste kindly supplied me with a large number of specimens of Homoptera, collected by him in the vicinity of Ankara, at Istanbul and its neighbourhood, as well as at Mersina. The Turkish material at my disposal is therefore more extensive than that available to any previous author on the same subject, which allows me to believe its detailed description may be of particular interest to entomologists.

At that time, however, I could not accomplish this task with the desirable degree of precision. In fact, the systematic study of the Homoptera, other than West European, has hitherto received so little attention, that every one dealing with any material of this group has really to achieve a pioneer task. Indeed, before arriving at the exact identification of any form present in a collection, and assigning it to its correct systematic position, a tremendous amount of preliminary work has to be done in each of the taxonomic groups involved. Thus, any faunistic account of extra-European Homoptera inevitably evolves into a long series of separate revisional studies, concerned with all the higher groups represented in the fauna. Consequently, the preparation of such an account may occupy several years.

The present paper is the first of a series of notes on the Homoptera of Turkey, which I hope to complete later. It contains a systematic treatment of some of the *Jassoidea* represented in the collections now available.

For the assistance which has made the present study possible, I wish to thank particularly Mr. W. E. China of the British Museum (Natural History), Dr. B. P. Uvarov, Mr. N. N. Jenjouriste, Prof. H. Ribaut, and Mr. H. Singh Pruthi; my thanks are also due to the authorities of the Zoological Museum of the Academy of Sciences of U.S.S.R. at Leningrad and of the Moscow University Zoological Museum, for the privilege of studying their respective collections of Homoptera.

I. *Chlorita* Fieber 1872 distinct from *Empoasca* Walsh 1862 with a new subgenus *Eremochlorita* Zakhvatkin. Fam. TYPHLOCYBIDAE (EMPOASCINAE).

Continuous field investigations on xerophilous EMPOASCINAE, together with a rather extensive study of their external anatomy, have led me to the following principal conclusions:—

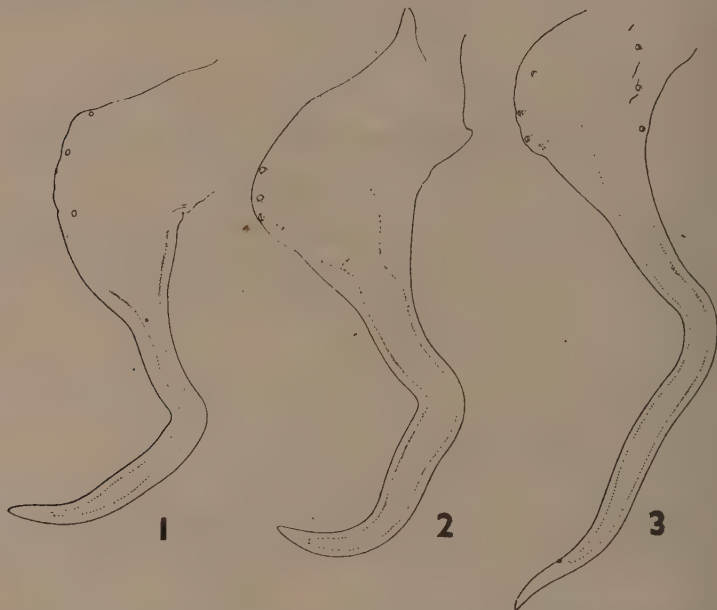
1. The majority of those forms must be severed either from *Empoasca* Walsh

TRANS. R. ENT. SOC. LOND. 97. PART 6. (SEPT. 1946). K

s.lat. or its existing subdivisions (*Empoasca* s.str., *Kybos* Fieber, *Hebata* Delong, *Idona* Delong) into a separate taxonomic unit of presumably generic value.

2. Within this genus the presence of two markedly different groups is evident, one of which is typified by *E. viridula* (Fallén, 1824) and the other by *E. tessellata* (Fieber) Lethierry, 1889.

3. The *tessellata*-group is composed of an unexpectedly large number of forms, closely similar in their external features, but sharply differentiated both ecologically and geographically, although they all live on *Artemisia* and most of them are definitely deserticolous.



FIGS. 1-3.—Process of tenth segment in, 1, *Chlorita* (*Eremochlorita*) *uvaroviana* sp. n. ♂; 2, *C. (E.) arenicola* sp. n.; 3, *C. (E.) tessellata* (Fieb.) Rib. ♂, from Naourzum, N.W. Kazakhstan.

4. Finally, the resemblance between the Palaearctic species of the *tessellata*-group and some of the Nearctic *Hebata* (namely, the *conspersa*-group) seems to be based only on ecological parallelism, as they exhibit no appreciable signs of a closer genetic affinity.

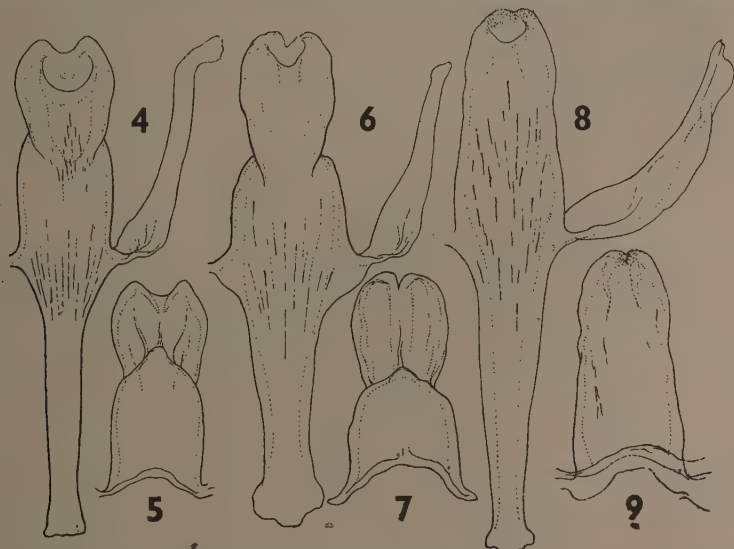
As *E. viridula* was long ago designated by Fieber (1866) as type of his genus *Chlorita*, it seems reasonable to restore this old generic name for the genus here discussed and respectively, in a subgeneric sense, for the former of its two subdivisions; as regards the latter subdivision, a new name, ***Eremochlorita*** subgen. n. is proposed. Type of the subgenus *C. (Eremochlorita) uvaroviana* sp. n.

Chlorita (Eremochlorita) uvaroviana sp. n. (figs. 1-9) may be distinguished from the numerous other members of this subgenus by the following characters:—

Size, medium for an *Eremochlorita*; stature relatively robust, the L/W ratio about 3.7 in the male and ranging from 3.47 to 3.77, with an average of 3.704, in the female.

General coloration light green, of a rather pure and vivid tint; hypodermal (whitish) ornamentation of head, pronotum and scutum not very conspicuous; darker maculae of tegmina fairly deep green, without a tendency to brownish. Lobes of the male pygophor prominently rounded, nearly rectangular, with some 10 sensory bristles at apex; processes of tenth segment (fig. 1) comparatively slender, obtusely angled at middle, with apical part slightly reflexed; aedeagus (figs. 4, 5) relatively short, distinctly subdivided by a deep constriction into a campanulate apical part and a somewhat larger basal piece, the dorsal wall of which is produced medially into a free conical protuberance.

Measurements. ♂: total length 2.25-2.30; width across eyes 0.62; length of vertex 0.14; inter-ocular width 0.33; length of pronotum 0.29; width of the same 0.55-0.57; length of tegmina 1.68-1.75 mm. ♀: total length 2.33-2.47 (average 2.431); width across



FIGS. 4-9.—4, Ventral view; 5, dorsal view of aedeagus of *Chlorita (Eremochlorita) uvaroviana* sp. n.; 6 and 7, the same of *C. (E.) arenicola* sp. n.; 8 and 9, the same of *C. (E.) tessellata* (Fieb.) Rib.

eyes 0.62-0.71; length of vertex 0.17-0.19; inter-ocular width 0.33-0.38; length of pronotum 0.31-0.33; width of the same 0.58-0.67; length of tegmina 1.86-2.00 mm.

Described from 2 males and 10 females taken by Dr. B. P. Uvarov 2.viii.1931 between Salihli and Borlu, in the Manisa province.

The closest relationship of *C. uvaroviana* is with a so far undescribed form of *Eremochlorita* from Transcaucasia, that may be regarded as conspecific with it, although representing a distinct geographical race. This new form, which I name *C. uvaroviana azerbeidzhanica* subsp. n., was found by me in the Mil Steppe, Azerbeidzhan, in 1931, where it occurs rather abundantly on *Artemisia scoparioides* Grossh.; it agrees very closely with the typical *uvaroviana* in all respects, except for its somewhat larger size (length of female 3.43-3.74, average 3.57 mm.) and less robust stature (L/W ratio of female 3.65-4.00, average 3.87). Furthermore, *E. uvaroviana* shows undeniable affinities with *C. arenicola* sp. n., another as yet undescribed form, inhabiting sandy deserts of the Astrakhan province and living on *Artemisia arenaria* D.C. and *A. scoparia*

W.K. *C. arenicola* is, however, distinctly larger and of a much deeper bright green colour and exhibits some additional differences from *uvaroviana* in the structure of the male genitalia (figs. 2, 6-7). At all events, as the two closest allies of the last-named species are distinctly confined to species of *Artemisia* belonging to the *Dracunculus* group, I think it highly probable that *C. u. uvaroviana* will also prove to live on some representative of the same section.

II. *Anatolidia* Zakhvatkin 1935 and other new subgenera of *Zyginidia* Haupt. Fam. TYPHLOCYBIDAE (ZYGINAE).

When erecting in 1935 (*Bull. Soc. nat. Moscou* 46 : 317-22) the new subgenus *Anatolidia* for the two very peculiar species of *Zyginidia* Haupt I described from Ankara, viz. *Z. obesa* and *Z. rostrata*, their connection with other members of this genus appeared to me very obscure. Of late, it has become evident that they are closely related to *Z. brevis* (Ribaut, 1931), a species hitherto known from southern France only, and which consequently must be transferred from the *parvula* group of *Zyginidia*, where it was placed by Professor Ribaut, to *Anatolidia*.

As a matter of fact, *Z. brevis* has, in common with the two Turkish species, most of the characters that seem to justify the separation of *Anatolidia* from either the true *Zyginidia* of the *scutellaris* type, on the one hand, and all the other groups of this highly polymorphic genus, on the other. These characters may be summarised as follows:—

Stature, decidedly more robust than in any other group of *Zyginidia*, the L/W ratio being usually less than 3 and the tegminal index not over 3; pronotum nearly parallel-sided, scarcely, if at all, broader posteriorly than head across eyes; tegmina with proximal section of CuA_1 much shorter than CuA_2 and the base of the fourth apical cell nearly square¹; hind-wings with proximal portion of Cu_1 (second cross-vein) interstitial in relation to the medio-cubital (first) cross-vein, and strongly oblique; basal processes of aedeagus fused with its canaliferous part, strongly reduced or absent.

Thus, representatives of *Anatolidia* prove to be much more widely spread in the Mediterranean subregion than was previously supposed. The relations of *Anatolidia* to its other congeners are stated in the following key, which summarises my conclusions on the subgeneric segregation of the East-Mediterranean *Zyginidia*.

- 1 (2). Exclusively graminicolous, very slender species without any definite black markings except on the mesonotum; the cross-veins of the hind-wings interstitial and almost rigorously transverse; head distinctly wider than pronotum across humeral angles, the latter nearly parallel-sided. *Zyginidia* Haupt. s.str.
- 2 (1). Species living on Dicotyledons; second cross-vein of the hind-wings always strongly oblique. Type of the subgenus, *Z. scutellaris* (Herrich-Schäffer, 1839).
- 3 (4). Second cross-vein of the hind-wings connected with M much more distad than the first, third apical cell of the tegmina very narrow and narrowed again before its end, vertex about twice as long medially as next the eyes, acutely angled anteriorly. Arbusticolous species

Fruticoidia subgen. n.

Type of the subgenus, *Z. bisignata* (Mulsant et Rey, 1859).

¹ It means their having a type of venation rather similar to that of the *maculata* group of *Erythroneura*, as figured, for example, by Beamer (1936, *Kansas Univ. Sci. Bull.* 24, fig. on p. 294), a very rare one among the Palaearctic ZYGINAE.

- 4 (3). Second cross-vein of the hind-wings connected with M, immediately beyond the point of insertion of the first, or slightly more distad; third apical cell of the tegmina not as above; vertex less than twice as long medially as next the eyes, more obtusely rounded anteriorly.
- 5 (6). Head and scutum without any dark markings or scutum with a single apical black dot; aedeagus tubular with two apical and no basal processes. Slender, very delicate and poorly pigmented species, whitish with vittae on clavus along its suture and two posteriorly divergent spots on pronotum bright orange red or yellow. Lives on certain Labiatae (*Mentha*, *Lycopus*, etc.) and some other herbaceous plants **Asianidia** subgen. n.
Type of the subgenus, *Z. asiatica* Kusnetzov, 1932.
- 6 (5). Upperside with a sharply contrasted dark pattern consisting of two large nearly circular spots on vertex, two basal spots on scutum and usually some more markings on pronotum; "labrum" entirely black; aedeagus more or less compressed laterally, without terminal processes. More robust, well sclerotised species, coloration not as above.
- 7 (8). Arboreal or arbusticolous species with sides of pronotum markedly divergent posteriorly; tegmina with the first section of Cu_1 about as long as Cu_2 and the base of the fourth apical cell always definitely angulate **Arboridia** subgen. n.
Type of the subgenus, *Z. parvula* (Boheman, 1845).
- 8 (7). Species living mainly on herbaceous plants, decidedly more robust in general appearance; with practically parallel-sided pronotum, first section of Cu_1 much shorter than Cu_2 , or Cu and M_2 : Cu_1 forming an almost continuous line, and base of the fourth apical cell nearly square **Anatolidia** Zakhvatkin, 1936.
Type of the subgenus *Z. obesa* Zakhvatkin, 1936.

Zyginidia (Arboridia) expansa sp. n. (figs. 10-13).

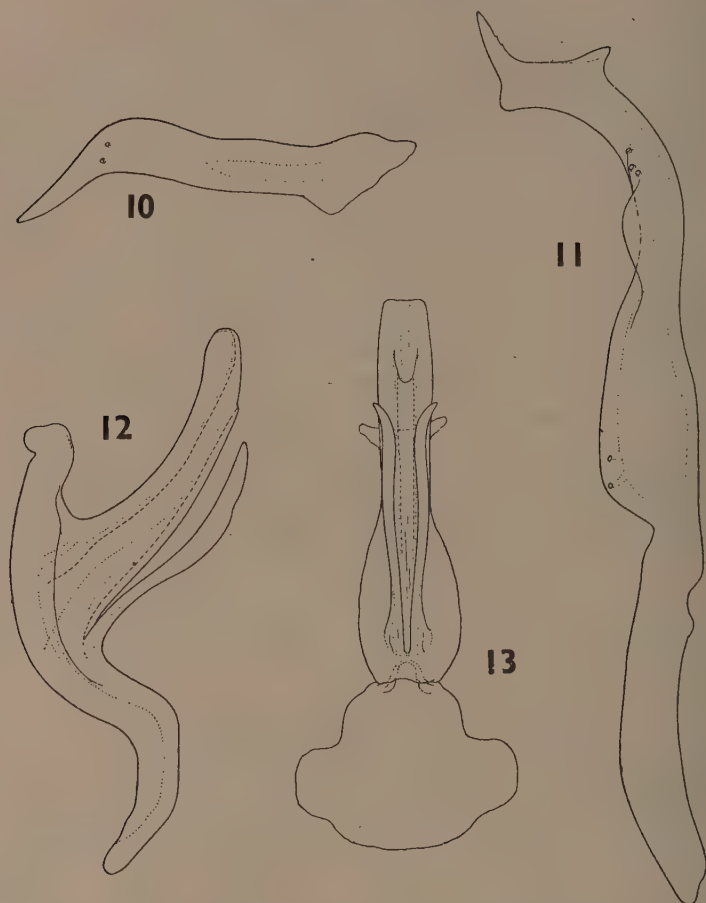
A small species, resembling the widely spread *Z. (A.) disjuncta* (Ribaut, 1931), but markedly divergent from it in the structure of the male genitalia and, especially, in that of the aedeagus.

♂. Coloration about as in *disjuncta*, with the orange red pigmentation strongly developed, as is usually the case in hibernating specimens of *Arboridia*. Stature rather robust, the L/W ratio being about 4.2; pronotum distinctly less than twice as long as vertex at middle (9:5) and somewhat less than twice as broad as long (17:9); tegminal index 3.73.

Lateral processes of pygophor (fig. 10) nearly as in *disjuncta*, but even longer and more distinctly curved apically; styles (fig. 11) also comparable with those of *disjuncta*, except that their distal portion is more elongate and the apical tooth appreciably longer; basal processes of aedeagus (figs. 12, 13) scimitar-shaped, arising close to the base of its canaliferous part, i.e. as in *parvula* and *erecta*, but afterwards deviating therefrom for a rather considerable distance; canaliferous part of aedeagus very slender and but feebly arched in a lateral view, though rather broadly expanded when viewed from below, with ventro-lateral edges almost foliaceous, which gives it a very peculiar appearance.

Measurements of the ♂ (holotype): total length 2.81; width across eyes 0.67; length of vertex 0.20; inter-ocular width 0.38; length of pronotum 0.36; width 0.67; length of tegmina 2.24; width about 0.60 mm.

There is before me a single male of this species taken at Ankara in December 1934 by Mr. Jenjouriste; it was caught under stones, i.e. in a hibernation refuge, in company with the two above-mentioned species of *Anatolidia*, *Mesagallia georgii* Zakhvatkin, *Hardya angorensis* Zakhvatkin, etc.



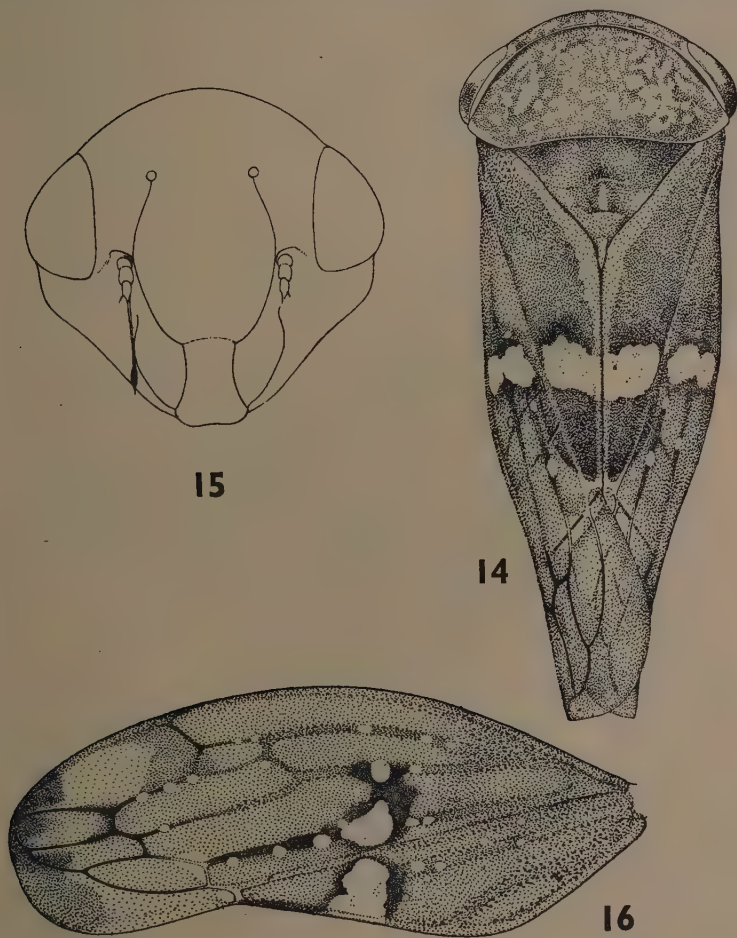
FIGS. 10-13.—*Zyginidia (Arboridia) expansa* sp. n. ♂. 10, Process of tenth segment; 11, style; 12, aedeagus, lateral view; 13, aedeagus, ventral view.

III. *Chunrocerus*, a new Genus, represented in Turkey by *Idiocerus balcanicus* Horváth (figs. 14-18). Fam. BYTHOSCOPIIDAE (IDIOCERINAE).

The striking brightly coloured species of IDIOCERINAE, described in 1903 by Horváth as *Idiocerus balcanicus*, and previously known only from Serbia, is found to extend its range eastwards as far as western Anatolia, where it has recently been discovered by Mr. Jenjouriste. The examination of Turkish specimens of *I. balcanicus* (which, of course, seem to be rather typical ones) clearly shows that the species dealt with does not belong to *Idiocerus* in the modern conception of this genus, i.e. as restricted by the late Professor Baker in his splendid work on Philippine IDIOCERINAE (1915, *Philipp. J. Sci.* 10 : 317-43). In fact, *I. balcanicus* is nothing else than a *Chunra* in Baker's extended interpretation of this genus, approaching even very closely to *C. niveosparsa*

(Lethierry, 1889), a well-known Oriental form, described at first as a species of *Idiocerus* by Lethierry.

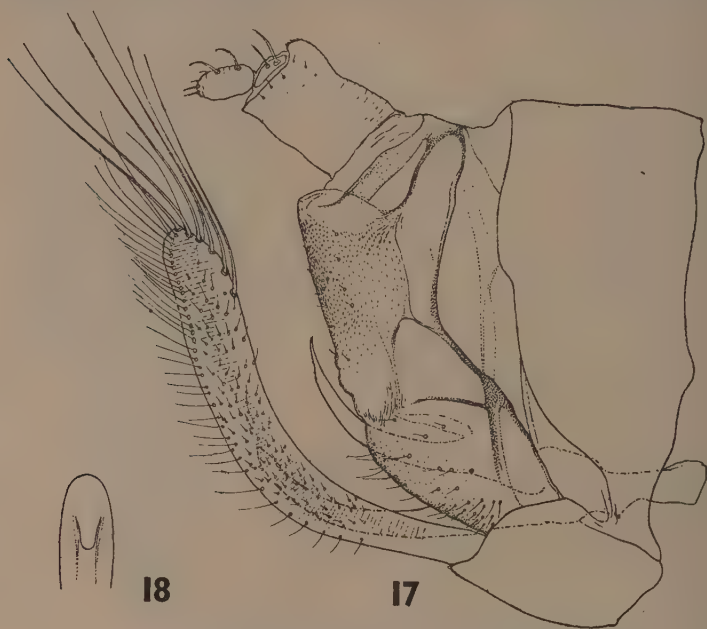
I cannot agree, however, with Baker's view that *niveosparsus* and its closest allies are true *Chunra*, congeneric with *C. puncticosta* (Walker, 1869), the type species of Distant's genus, and, consequently, I shall abstain from referring



FIGS. 14-16.—*Chunrocerus balcanicus* (Horváth). 14, male; 15, ♂ face; 16, ♀ tegmen.

balcanicus to *Chunra*. In my opinion, both the *niveosparsus* group and *balcanicus* differ very substantially from typical *Chunra*, and are to be regarded as constituting a separate genus, which I propose to name **Chunrocerus** gen. n. So far as can be ascertained from the materials and information at my disposal, this new genus chiefly differs from *Chunra* Distant, 1907, in the following features :—

Distance between ocelli about one and a half times more than the distance from ocellus to eye. Pronotum three to nearly five times longer than vertex. Scutum obviously smaller in size, shorter than pronotum and vertex together, but feebly raised basally or practically flat, of the most ordinary triangular shape. First apical cross-vein of tegmina closely approximated to the point of bifurcation of the radial vein, which gives the following results: (1) the first subapical cell is very small, always much smaller than the other tegmen cell, and even tends to become vestigial; (2) this small cell is much narrower at its base than apically; (3) finally, the first apical cell acquires a correspondingly much greater length, exceeding that of the second and extending proximally up to the middle



FIGS. 17-18.—*Chunrocerus balcanicus* (Horváth). 17, ♂ genitalia; 18, tip of aedeagus.

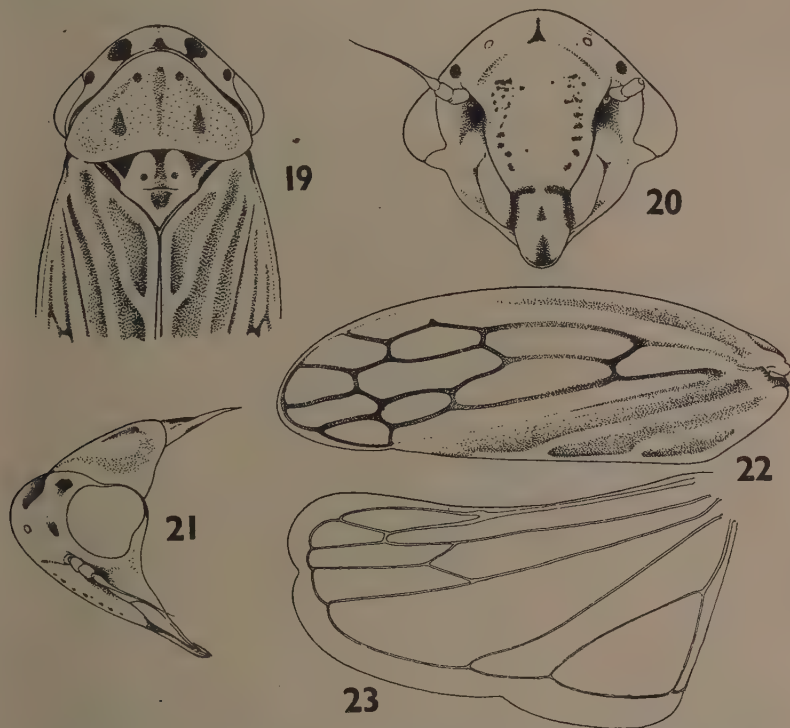
of the second subapical cell, or eventually still farther again. Medio-cubital cross-vein of tegmina connected with M at about middle of the discoidal cell, the latter being long and narrow, of an almost lanceolate shape. Distal end of CuA_1 , lying on a much higher level than those of M_{2+3} and R_{4+5} , the fourth apical cell thus spreading distad only up to the middle of the inner margin of the third, and the apex of the membrana being correspondingly rather narrowly rounded. Appendix very broad, with greatest width in its distal third. Clavus broadening to about two-fifths of its length, then gradually narrowing to apex. General type of coloration essentially distinct from that of *Chunra* in the absence of dark stripes on head, pronotum and scutum and the peculiar snow-white callose ornamentation of the tegmina.

Type of the genus, *Idiocerus niveosparsus* Lethierry, 1889.

As will clearly be seen from this description and the accompanying figures of the main structural details of *C. balcanicus* Horváth, as well as from the respective figures of *C. philippinensis* Baker, *C. lagunensis* Baker and *C. palawanensis* Baker in Baker's monograph, *Chunrocerus* exhibits appreciably

more idioceroid features than the genuine *Chunra* Distant of the *puncticosta* Walker type, or than the species of *Ipocerus* Baker, *Iposcopus* Baker and the recently described *Megipocerus mordvilko* Zakhvatkin. The scutum, for instance, is in this case of a most generalised type, approaching much more closely to that of the normal IDIOCERINAE than to its exaggerated condition and peculiar form, found in the last-named genera; the shape of the body is definitely more idioceroid, the male antennae bear the same plate as in *Idiocerus* s.str., etc. Thus, it may be placed nearer to *Idiocerus* than to *Chunra* and its nearest relatives, and should be considered as a connecting link between the two groups of genera.

So far as I am aware, the Mediterranean *Idiocerus notatus* Fabricius shows rather marked similarity to *Chunrocerus*, and may possibly belong to this genus. The latter suggestion cannot, however, be ascertained until this species has been more carefully studied.



FIGS. 19-23.—*Mesagallia georgii* gen. et sp. n., female. 19, Fore part of body, dorsal view; 20, face; 21, head and thorax, lateral view; 22, tegmen; 23, hind-wing.

IV. New genera and species of AGALLIINAE. (Fam. BYTHOSCOPIIDAE.)

Mesagallia gen. n. (figs. 19-23).

During his winter excursions in the neighbourhood of Ankara, Mr. Jenjouriste happened to find two females of a very peculiar small species of

AGALLIINAE, which at first glance might easily be mistaken for a member of the *Aceratagallia* stock (of which it has the size, main proportions and general appearance), but on closer examination proves to represent an undescribed genus, allied to *Durgades* Distant. This new genus, which I propose to term *Mesagallia*, may be characterised as follows:—

♀. Size, exceptionally small for a representative of the tribe Nehelini, not exceeding 3.7 mm.; stature robust, eusceloid. Vertex parabolically produced before eyes about twice its own length, medially slightly longer than next the eyes or of nearly uniform length throughout its width, three and one-half to four times shorter than pronotum; posterior margin of vertex typically neheloid, viz. sinuately curved laterally and extending some distance behind the eyes; the latter relatively small, strongly oblique and extending backwards up to six-sevenths of the pronotal length. Distance between ocelli about one and a half times more than that from ocellus to eye. Face comparatively short, not fully as long as wide across eyes; fronto-clypeus moderately convex, with lateral edges not expanded above the antennal sockets and lateral sutures noticeably arcuate; clypeal suture fairly distinct, surface of head finely shagreened except for the apex, which is smooth and obviously shining.

Pronotum nearly twice as broad as long, with anterior margin strongly protruded, cephalad in the middle and sinuate laterally, according to the sigmoid curve of the postocular part of vertex; with lateral margins subevanescent, and moderately concave hind margin. Surface of pronotum uniformly finely shagreened, entirely opaque.

Tegmina coriaceous, comparatively broad, with costal margin rather strongly convex and apex narrowly rounded; venation very conspicuous though not raised at all, dark on a pale ground: R_1 vestigial, but quite distinct basally; two cross-veins between M and Cu and none on the clavus; no additional veinlets. Hind-wings with apex strongly bilobate and second apical cell fairly large; the first anal vein bifurcates before the middle of its length.

Armature of legs as in other Nehelini, viz. hind tibiae with 7 to 8 bristles on their dorso-external edge, 7 bristles on the ventro-external and 8 on the dorso-internal one.

Ground colour light ochreous with dark pattern as in *Durgades*, but even more sharply contrasted.

Type of the genus, *Mesagallia georgii* sp. n.

As has been already mentioned, *Mesagallia* appears to be closely allied to the Agallian genus *Durgades* Distant, 1912, which is generally considered as consisting of only three purely Himalayan species (*D. nigropictus* Distant, 1912, the type of the genus, *D. mirabilis* Pruthi, 1930, and *D. idiocerus* Pruthi, 1930); in my opinion, however, it includes, in addition, the unexpectedly numerous forms hitherto confused under the name "*Agallia reticulata*,"² *Mesagallia* is chiefly distinguished from *Durgades* by its small size, the eusceloid shape of body, in the absence of cross-veins and a relatively much longer vertex; in most of the other characters it agrees almost perfectly with *Durgades* s.str.

Besides *M. georgii*, I am acquainted with two more species of *Mesagallia*, which are also represented in the material at hand by female specimens only. One of them was collected by Professor A. N. Kiritschenko in the vicinity of Vladikavkaz and the second at Paraga, near Ordubad, Nakhitshevan U.S.S.R., by the late Mr. Znoiko. Thus it appears that *Mesagallia* is rather widely distributed throughout Caucasus and Asia Minor.

² These forms, though very similar to the typical (Himalayan) species of *Durgades* in all essentials, may be considered as forming a separate subgenus, *Dryodurgades* subgen. n. type *Agallia reticulata* H. S.

Mesagallia georgii sp. n.

♀. Stature comparatively robust, the L/W ratio being almost exactly 3.0; vertex medially about as long as next the eyes, 3.5 to 3.7 times shorter than pronotum; the latter somewhat more than twice as broad as long (96 : 45); tegmina extending fairly well beyond tip of abdomen, about 2.95 times as long as wide. Subgenital plate slightly convex posteriorly.

General colour of the upperside whitish-ochraceous; vertex light ochreous inclining to chrome yellow on its shining apical area and of a duller tint on the remainder of surface; scutum of a similar chrome-yellowish tone but somewhat paler; underside and legs pale yellowish. Vertex with a small median spot on its posterior edge and, each side of middle, with a large roundish spot extending backwards to its carinated hind margin and slightly expanded over the latter, and another much smaller dot close to the eye, black. Facial black pattern consisting of an unpaired triangular frontal spot, two more between each ocellus and eye, moderately coloured remains of the metopial suture, numerous dots on the lateral parts of clypeus, very large subantennal spots narrowly prolonged along the lateral sutures of clypeus, and some more indefinite markings on genae; moreover, the "labrum" is broadly margined with fuscous in its basal half and bears two almost triangular median spots, of which the apical is the largest.

Pronotum with a longitudinal median vitta, two circular dots close to its anterior end and two more widely separated triangular spots behind middle, deep sepia brown, and its lateral parts with a rather indefinite ferruginous sigmoid figure on each side. Scutum with a complex black pattern formed by a small median triangle produced caudad into a narrow longitudinal stripe, by two very large basal spots extending sideways to its lateral edges but interrupted by the yellow submarginal carinae, by two roundish dots cephalad to the scutellar suture, as well as by this suture itself and a spot posterior to it.

Tegmina with the venation of corium and membrana deep sepia brown and claval veins together with the interior half of the claval commissure, broadly whitish; claval cells filled with brown ranging in tone from cinnamon and light ferruginous to sepia, the deepest coloured parts being the base of the first, the apical portion of the second and in a lesser degree, that of the third claval cells. Hind-wings whitish subhyaline with the venation almost concolorous.

Legs rather irregularly spotted with fuscous. Underside of thorax and abdomen with various brownish markings; subgenital plate of the ground colour, with a ferruginous median and two lateral spots.

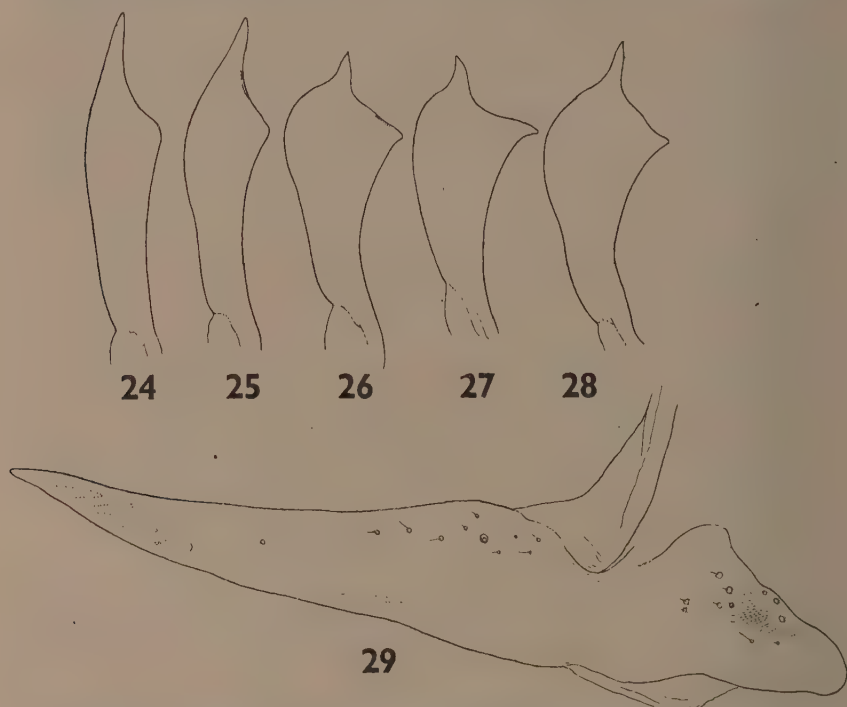
Measurements: total length 3.43-3.45; width across eyes 1.14; length of vertex 0.15; inter-ocular width 0.76-0.77; length of pronotum 0.52; width 1.01-1.04; length of tegmina 2.80-2.82; width 0.95 mm.

I dedicate this species to my little son George.

Anaceratagallia gen. n. *laevis acuteangulata* subsp. n. (figs. 24-28).

The numerous Palaearctic species of the old genus *Agallia* auctt., centring about *A. venosa* (Fallén, 1824) as type, are so obviously similar to *Aceratagallia* Kirkaldy, 1907 (type of the genus *Bythoscopus sanguinolentus* Prov. 1872; a Nearctic species), in their general appearance, that Mr. Oman (1936, *Univ. Kansas Sci. Bull.* 37 : 350) found it possible to include them in this genus. In my opinion, however, Mr. Oman's idea of this genus is too wide, as the Palaearctic species of the *venosa* group exhibit a number of very substantial differences from the typical (Nearctic) *Aceratagallia*, being actually much more remote from them than from the true *Agallia* Curtis (*i.e.* from the species of the *A. puncticeps* Germar group), which seems to be also an exclusively Old World genus. It

appears more correct to regard the *venosa* group as a separate generic unit, merely parallel or analogous to *Aceratagallia* than identical with it. Hence, the term **Anaceratagallia** gen. n. (type of the genus, *A. venosa* Fallén, 1824) is proposed for its designation.



FIGS. 24-29.—♂ pygophor process in *Anaceratagallia laevis laevis* (Rib.) from Southern France (24, 25); in *A. l. acuteangulata* sp. n. from Bujuk-Dere (26, 27); and from Genzano, near Rome (28). 29, *Selenocephalus uvarovi* sp. n. ♂, lobe of pygophor.

The principal differences between the two genera discussed may be shortly summarised as follows:—

1. Vertex and fronto-clypeus finely, but rather conspicuously punctuated, with interspaces between the puncta smooth and obviously shining. Upper exterior edge of the hind tibiae with 11 to 13 bristles in a row. Male genital plates lying in a common horizontal plane, fused together along their inner margins to a variable length, and lacking any kind of large bristles on their ventral surface; processes of the tenth segment very slender, usually, straight, styles unforked. Female subgenital plate usually notched at middle *Aceratagallia* Kirkaldy.
- Vertex and fronto-clypeus throughout finely shagreened, without any appreciable punctuation. Upper exterior edge of the hind tibiae with 8 to 9 bristles in a row. Male genital plates steeply tectiform, free from the base, with several large bristles disposed in a submedian longitudinal row; processes of the tenth segment variable in shape, but never as above. Hind margin of the female subgenital plate almost straight *Anaceratagallia* gen. n.

As defined in the key, the last-named genus is apparently a strictly Palaearctic group and *Aceratagallia* a merely Nearctic, while the latter is found to be represented by an isolated species in the fauna of the Eremian subregion.

In the available Turkish material, I find two species of *Anaceratagallia*, *A. ribauti* (Ossian, 1939), and *A. laevis* (Ribaut, 1935), the former being represented by its nominal (southern) race, while the latter appears to be racially distinct from typical examples of *A. laevis laevis* (from Southern France and Northern Italy). It may be characterised as follows:—

A. laevis acuteangulata subsp. n.

Distinguishable from the nominal form of *laevis*, which seems to be confined to the north-western part of this species' area, in being, on the average, somewhat larger (males 3.04–3.57; females 3.33–3.80 mm.) and slightly less robust (L/W ratio of male 2.87–3.00, of female 2.80–2.95); in the more elongated tegmina, the index of which ranges, in the male, from 2.85 to 3.03, and in the female from 2.74 to about 2.30; and in the processes of the male tenth segment being much more dilated in their apical half, with upper angle strongly prominent and usually acutely pointed, and the apical tooth relatively very short (figs. 26–28).

In *A. laevis laevis*, the length of the males is usually about 3.0–3.20 mm., of the females 3.18–3.40 mm., the L/W ratio 2.80–2.85 and 2.68–2.80 respectively, the tegminal index of the male not above 2.30, of the female 2.63–2.80; moreover, the processes of the male tenth segment are decidedly less expanded (being, consequently, more elongate in form) with upper angle obtuse and apical tooth comparatively long (figs. 24, 25).

The above description is based on several males and females from Bujuk-Dere near Istanbul, which may be considered as the typical locality of this race, and some more females from Burnova near Smyrna, 16 and 25.vii.1931 (B. P. Uvarov). *A. l. acuteangulata* is also known to occur in Greece (where it is apparently represented by a slightly different subrace) and from several localities of Central and Southern Italy.

V. *Selenocephalus stenopterus* (Fieber) Signoret and its Eastern Geographical Races and a new Turkish species of the genus. Fam. EUSCELIDAE.

S. stenopterus Fieber must be considered as one of the most sharply defined species of *Selenocephalus* Germar; it differs fundamentally in many respects from all its Palaearctic congeners, and occupies among them a rather isolated position. It is characterised by its comparatively very slender proportions, the L/W ratio being always higher than 3.0; narrow, strongly elongated tegmina with their index ranging from 3.18 to about 3.5; a quite peculiar type of coloration, i.e. the presence of a whitish, triangular macula on the tegmina; the structure of the male genitalia, and, especially, that of the aedeagus; and, finally, in the type of its geographical area.

S. stenopterus is by no means synonymous with *S. pallidus* Kirschbaum, 1868, as was quite arbitrarily suggested by Horváth in 1897, and up to now generally accepted. Indeed, the very imperfectly known Kirschbaum species has apparently no appreciable affinities with that of Fieber and of Signoret, as none of the features, mentioned in the former author's original description, agrees with those of *stenopterus*, and many of them even display quite opposite features. *S. pallidus* is characterised, for example, by the shortness of its tegmina, being "sehr wenig länger als d. Hinterleib"; by the uniform pale

coloration of the upperside ("oben ganz blass gelblich"); by its comparatively small size (7 mm.), etc. Thus, it appears firstly, that this species is a true member of the *griseus* group; secondly, that it exhibits marked affinities with the smaller species of the latter group, dealt with elsewhere³; and, finally, that it is not identical with any of them.

The area of distribution of *S. stenopterus* includes Greece, Yugoslavia, Asia Minor and the U.S.S.R., although no definite data on its occurrence in this country have ever been published. Records for Hungary relate to *S. pallidus*, and those for Tunisia are doubtless incorrect. I personally know this species from Crimea, from the Caucasian Black Sea coast (where it appears to be rather frequent) and from Western Anatolia; thus, the distribution of *stenopterus* is clearly Balcano-Anatolian in its general outlines.

The question as to the typical locality of *stenopterus* involves certain difficulties due to the fact that it was first recognised by Fieber from material coming from Greece and Dalmatia (Katalog. Europ. Cicad. p. 10; 1872), while Signoret's description of this species appears to be founded solely on Trebizond specimens. However, as it seems more correct to regard the latter as actual types of *stenopterus*, Trebizond may be considered as its *locus classicus* and, consequently, its eastern Pontian race as the nominal one.

Judging from Signoret's description and figures, this eastern race is characterised by its medium size (male 7 mm., female 9½ mm.), rather rich coloration and a tegminal index about 3.3. If it be true, my Abkhazian examples of *stenopterus* from Gagry (Uljanin, 1867) and some other localities of the Caucasian Black Sea shore may also be referred to its nominal form, as they exhibit precisely the same features as have just been mentioned. The total length of the Abkhazian females ranges from 8.36 to 8.57 mm., with an average of 8.408, and that of the (unique) male is 7.36 mm.; the tegminal index of females varies from 3.20 to 3.32 with an average of 3.225; they are, moreover, distinctly darker than the other races of *stenopterus*, being ochraceous tawny with dark pigmentation relatively well developed and the underside very markedly infusate. Additional evidence in favour of the opinion as to the racial identity of Abkhazian and Trebizond specimens of *stenopterus* is that the two localities are very close to each other in respect of their fauna, as the two belong to the same very natural and homogeneous biogeographical unit, the lowland Pontian province of Uvarov (1921).

The second geographical race of *stenopterus* with which I am acquainted is represented in the material studied by a single female caught by Dr. B. P. Uvarov at Demirchi, S. of Simav, at an altitude of about 3000 ft., 3-4.viii.1931. It differs markedly from typical females of *S. stenopterus* in the following particulars:—

Stature, comparatively much more slender, the L/W ratio being as high as 3.14 and the tegminal index about 3.45. General coloration very pale; ground colour honey yellow, dark ornamentation rather poorly developed. Size distinctly larger than in the nominal form, the measurements of the holotype being as follows: Total length 8.84; width across eyes 2.82; length of vertex 0.46; inter-ocular width 1.76; length of pronotum 1.10; width 2.68; length of tegmina 7.30; width 2.11 mm.

The morphological distinctness of this specimen, coupled with the evidence that it represents a highland form, allows me to consider it as a separate sub-species of *stenopterus*, which may be termed *S. s. simavensis* subsp. n.

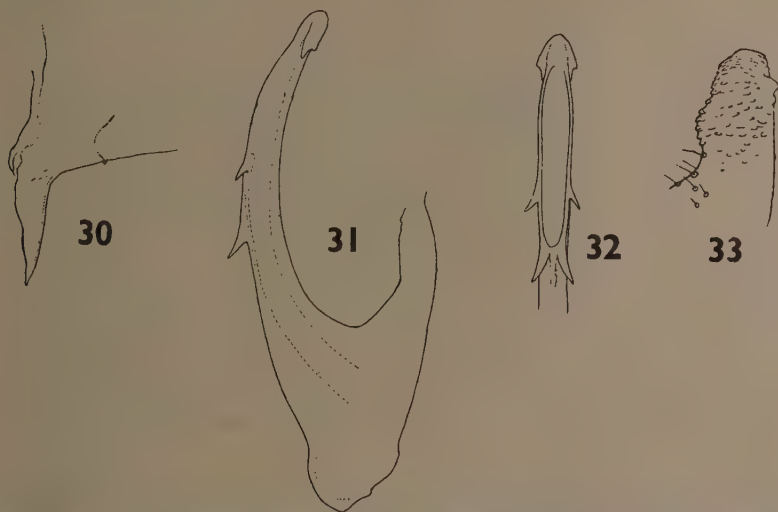
³ On Some European Species of *Selenocephalus*. Zakhvatkin 1945, *Proc. R. ent. Soc. Lond. (B)*, 14: 6-9.

The third eastern race of *stenopterus*, ***S. s. tauricus*** subsp. n., inhabits Crimea or, more precisely, its southern Coastal district. This form is nearly as pale as *simavensis*, while of a slightly different tinge, somewhat intermediate between Ridgeway's ochraceous-buff and Antimony yellow (pl. XV); it is, moreover, very distinctly smaller than *simavensis*, the total length of females being 7.66–8.40, with an average of 7.982 mm., and somewhat less slender, as its tegminal index ranges in that sex from 3.22 to 3.34, with an average of 3.308. The type locality of this subspecies is Karadagh, where it seems to be rather abundant.

Thus, *S. stenopterus* is represented in the eastern (Euxinian) part of its area by at least three apparently well-defined geographical races. Unfortunately, nothing is known about the more western Greek and Yugoslavian forms of this species, which probably may prove to be racially distinct from the eastern and northern ones.

***Selenocephalus* (s.str.) *uvarovi* sp. n. (figs. 29–33).**

This small, rather strongly sexually dimorphic species was collected by Dr. B. P. Uvarov at Goelchik, Bozdagh Mountains, Smyrna Province, 29.vii.1931 : 1 male and 2 females.



FIGS. 30–33.—*Selenocephalus uvarovi* sp. n. ♂. Ventral spine of anal tube (30); aedeagus lateral view (31); aedeagus, ventral view (32); distal portion of style (33).

♂. Similar in coloration to dark specimens of *S. griseus* Fabricius and its nearest allies, with subapical whitish areas on tegmina rather conspicuous.

Size, relatively very small; form moderately robust, somewhat more slender than in the genuine *S. griseus* Fabricius⁴; the L/W ratio being equal to 2.71. Vertex about three times as wide as long in middle, where it is about 1.6 times longer than next the eyes (23 : 14). Fronto-clypeus as long as wide at level of the antennal sockets, and exactly

⁴ Zakhvatkin : *On Some European Species of Selenocephalus*. Zakhvatkin 1945, *Proc. R. ent. Soc. Lond. (B)*, 14 : 6–9.

twice as long as anteclypeus, with a very conspicuous apical fovea; lateral sutures of anteclypeus slightly convex throughout their length, its greatest width lying therefore nearly at middle of its length. Pronotum noticeably less than twice as long as vertex (42 : 23) and nearly two and a half times broader than long in middle. Tegmina extending well beyond tip of abdomen, rather elongate, glabrous; tegminal index about 2.9.

Lobes of the genital segment (fig. 29) very narrow, blade-shaped, gradually tapering to the end, with dorsal margin practically straight and the microchetae of their external surface scattered along two-thirds of their whole length. Ventral spines of the tenth segment (fig. 30) comparatively long, slender and nearly straight. Genital plates (fig. 31) almost triangular, with lateral margins slightly convex and apices narrowly rounded. Styles relatively slender, posterior portion very roughly squamate (fig. 32). Aedeagus (fig. 33) very slender, evenly arched throughout its length with two widely spaced pairs of spines, the upper of which assume, in a lateral view, a decidedly marginal position.

Measurements of the holotype: Total length 6.07; width across eyes about 2.25; length of vertex 0.50; inter-ocular width 1.54; length of pronotum 0.92; width 2.16; length of tegmina 4.84; width 1.67 mm.

♀. Entirely pale, tawny ochraceous, with usual dark markings on face and a few widely scattered obsolete brownish vermiculations at apex of clavus and on membrana; hind-wings strongly infusate; dorsum infusate, mesopleurae with some indefinite brownish spots.

Size, distinctly larger than in the male; general proportions appearing at first glance quite different because of an appreciable degree of brachypterism, but in reality closely approaching those of the male, the L/W ratio being 2.73 in its standard computation, and 2.8, if calculated to the somewhat exerted tip of ovipositor. Vertex medially one and two-thirds as long as next the eyes and about two and two-thirds as wide as long in middle. Fronto-clypeus with its apical fovea even deeper than in the male, distinctly shorter medially than broad at level of the antennal sockets (26 : 29), and somewhat more than twice as long as anteclypeus (58 : 27); the latter slightly narrower than in the male but of a quite similar form. Pronotum in middle 1.6 times as long as vertex and about two and a half times broader than long. Tegmina but slightly less elongate than in male (tegminal index 2.72), although they scarcely if at all reach the tip of abdomen. Subgenital plate nearly as in *griseus* but with its submarginal dark transverse line extending not so far sideways as in the latter species.

Measurements of the allotype: Total length 7.22; width across eyes 2.64; length of vertex 0.66; inter-ocular width 1.76; length of pronotum 1.06; width 2.60; length of tegmina 5.63; width 2.07 mm.

S. uvarovi seems to me very closely related to *S. pallidus* Kirschbaum, 1868, an imperfectly known, nearly forgotten species, described long ago from a single female from Budapest and yet not recognised as valid; as has been already mentioned (p. 161), it is generally considered as identical with *S. stenopterus*, which is obviously not the case. On the other hand, *S. pallidus* is by no means synonymous with *S. griseus*, as has been suggested by Signoret, being essentially distinguishable from it in all the features mentioned in Kirschbaum's original description, and is clearly not identical with *S. conspersus* (Herrich-Schäffer)⁴; in my opinion, *S. pallidus* must be regarded as a distinct and even well-defined species of *Selenocephalus*. Some of the most noteworthy features of *pallidus* have already been discussed in the foregoing note on *S. stenopterus*, which makes it unnecessary to repeat them here; it must be added, however, that the present species is furthermore characterised by entirely hyaline hind-wings, a greater length of vertex in comparison with *S. griseus*, and rather elongate proportions of the face.

⁴ Zakhvatkin: *On Some European Species of Selenocephalus*. Zakhvatkin 1945, *Proc. R. ent. Soc. Lond.* (B), 14: 6-9.

In most of its features, the female of *S. uvarovi* perfectly agrees with Kirschbaum's description of *pallidus*, namely in size, general proportions, including the relative shortness of the tegmina, and coloration, so that a genuine affinity between them appears to me certain; however, they cannot be considered as identical, for *S. uvarovi* possesses dark-coloured hind-wings, is apparently even more brachypterous and probably agrees more closely in its face proportions with *griseus*, than it does with *S. pallidus*. In my opinion, therefore, the two species discussed may be regarded as closely akin and representing a distinct group of forms within the limits of the genus *Selinocephalus*. It is to be presumed that the same degree of sexual dimorphism as in *uvarovi* will be found to characterise *pallidus* as well.

The second species of *Selinocephalus* displaying undeniable affinities with *uvarovi* is *S. conspersus* (Herrich-Schäffer, 1835), an equally misinterpreted form, the systematic status of which is discussed at length elsewhere.⁴ *S. conspersus* is also characterised by its small size (6.4–6.7 mm. in the male, and 7.3–7.4 mm. in the female) and exhibits some resemblances to *uvarovi* in the structure of the male genitalia, especially that of the aedeagus. However, *conspersus* greatly differs from the last-named species in the absence of any appreciable degree of sexual dimorphism in proportions and coloration, the two sexes being in this case almost equally slender, long-winged and dark coloured. Thus the relations between *S. uvarovi* and *conspersus* are evidently rather remote.

VI. New subgenera and species of the genus *Hardya* Edwards 1922 from S.E. Europe and Western and Middle Asia (figs. 34–62). Fam. EUSCELIDAE.

Difficulties that have arisen in an attempt at a precise identification of some female specimens of *Hardya* from Turkey have led me to a decision to undertake a revisional study of the whole available East Mediterranean material of this genus, the results of which form the subject of the present note.

Although only a few closely related species of *Hardya* are known to occur in Western Europe, this genus is represented in South-Eastern Europe, Western and Middle Asia by a great variety of forms, some of which are so dissimilar from its typical members that they undoubtedly deserve to be treated as representing separate subgenera. In the material under study, no less than seven different forms of *Hardya* are present that may be arranged into three subgenera: *Hardya* s.str., *Eohardya* subgen. n. and *Mimohardya* subgen. n.

1. *Hardya* s.str.

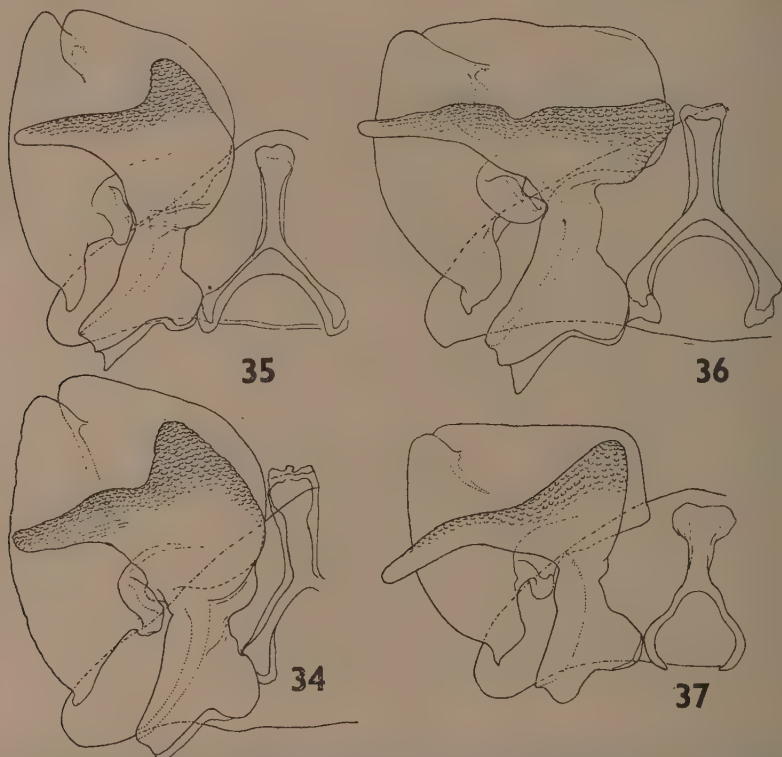
The numerous members of this subgenus are variable in size, stature and proportions, but rather uniform in their structural features and coloration, being certainly more adequately typified by *H. tenuis* (Germar) than by the actual genotype of *Hardya*, *H. melanopsis* (Hardy). They have in common the following characters:—

Vertex of medium length, usually less than two-thirds of the middle length of pronotum and of the inter-ocular width. Tegmina with first subapical cell more or less lanceolate and occasionally shortly stalked and the apical cells relatively long. General coloration moderately contrasted, with the whitish areas of head and tegmina rather obsolete; dark

⁴ Zakhvatkin: On Some European Species of *Selinocephalus*. Zakhvatkin 1945, Proc. R. ent. Soc. Lond. (B), 14: 6–9.

pattern of tegmina of a most generalised type, reaching its highest intensity in the third apical cell, which is usually entirely filled up with fuscous. Female subgenital plate black with paired ochreous spots at base and no median spot at hind margin.

♂. Genital plates highly modified, of a very peculiar bilobed form, with inner edges strongly diverging posteriorly; lobes of the genital segment forming apically a heavily sclerotised comb, consisting of 8 to 13 teeth and variable in shape from one species to another; styles with distal portion directed at right angles to the longitudinal axis of body, roughly squamate, of a variable, but always quite original form; aedeagus simple, abruptly narrowed and nearly right angled at middle, with its tubular distal part rather slender, and a claw-like apex.



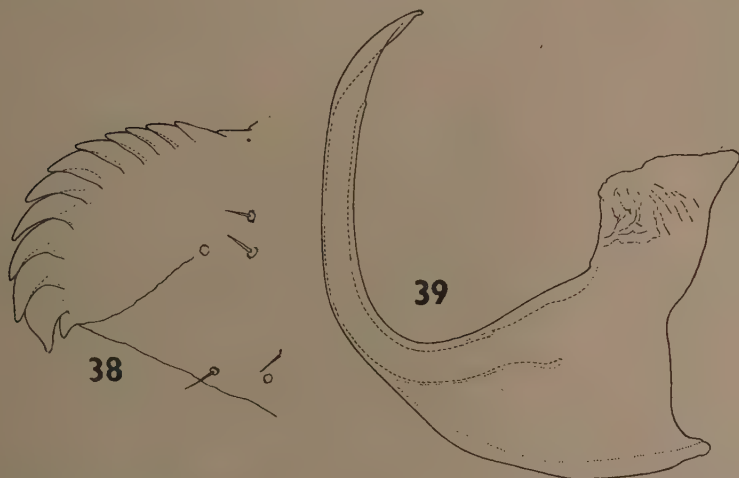
FIGS. 34-37.—Styles, connective and outlines of the ♂ genital plates of: 34, *Hardya iranica* sp. n.; 35, *H. turanica* sp. n.; 36, *H. tenuis* (Germar); 37, *H. sevaniensis* sp. n.

In the area here discussed this group is represented, firstly, by the following three new species, extremely like *H. tenuis* in their general appearance, and apparently hitherto confused with it.

***H. (s.str.) iranica* sp. n.**

A rather large and slender species, practically indistinguishable from *H. tenuis* in size, proportions and other external features, but widely differing therefrom in the structure of the male genitalia.

♂. L/W ratio ranging from 3.53 to 3.64, with an average of about 3.58; tegminal index 3.42-3.54 (average 3.47). Genital plates (fig. 34) distinctly more elongated than in *tenuis*, i.e. very appreciably longer than broad (30 : 23), with posterior margin oblique and passing rather insensibly into their broadly rounded inner edge, without forming with it any noticeable angle. Comb of genital lobes (fig. 38) consisting of about 13 very broad, strongly imbricated teeth, gradually increasing in size up to the penultimate (which, however, markedly differs from the other in its shape) and with the ultimate tooth being the smallest. Styles (fig. 34) with distal portion produced caudad into a large triangular lobe and external (apical) process sinuately curved. Aedeagus (fig. 39) similar to that of *tenuis* in general shape, but with its claw-like apex much more curved and having its posterior wall obviously thickened. The male genitalia of *tenuis*, not previously figured, are shown in figs. 36, 40 and 44 for the sake of comparison.



Figs. 38-39.—*Hardya iranicola* sp. n. ♂, 38, comb of pygophor lobe; 39, aedeagus.

♀. L/W ratio 3.46-3.76, average 3.59; tegminal index 3.20-3.40 (average 3.34). Subgenital plate as in *tenuis*, with lateral angles produced into almost rectangular lobes.

Measurements. ♂. Total length 3.43-(3.497)-3.65; width across eyes 0.96-1.01; length of vertex 0.26-0.29; inter-ocular width 0.42-0.46; length of pronotum 0.44-0.48, width 0.92-0.97; length of tegmina 2.77-(2.892)-3.04, width 0.81-0.88 mm.

♀. Total length 3.65-(3.765)-3.87; width across eyes 1.01-1.10; length of vertex 0.29-0.31; inter-ocular width 0.48-0.53; length of pronotum 0.48-0.53, width 0.97-1.06; length of tegmina 2.95-(3.065)-3.17, width 0.92-0.94 mm.

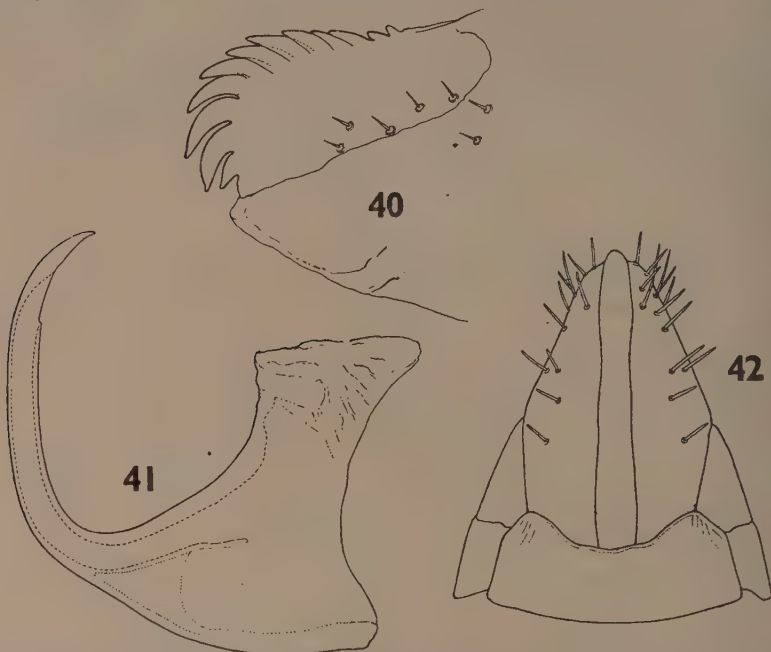
Described from 4 males and 7 females captured at Zergendeh, N.W. Persia, in December 1934.

H. (s.str.) turanica sp. n.

Very similar to the preceding species of which it possibly represents a geographical race only, but distinctly smaller and with somewhat different male genitalia.

♂. L/W ratio 3.39-3.50, average 3.46; tegminal index about 3.23. Genital plates as in *iranicola*, but even narrower (ratio 27 : 20) and with posterior margin more oblique (fig. 35). Comb of the genital lobes (fig. 40) strongly rounded in its general outline, with

its last 5 teeth free from their base (not imbricated at all) and the penultimate (subapical) tooth similar to the foregoing in form and size. Aedeagus (fig. 41) and styles (fig. 35) similar to those of *iranicola*, but the latter with caudal lobe smaller and external process nearly straight.



Figs. 40-42.—*H. turanica* sp. n. ♂, 40, comb of pygophor lobe; 41, aedeagus; 42, ♀ subgenital plate.

♀. L/W ratio 3.40-3.56, average about 3.51; tegminal index 3.24-3.40, average 3.31. Subgenital plate precisely as in *iranicola* (fig. 42).

Measurements. ♂. Total length 3.28-(3.313)-3.36; width across eyes 0.94-0.97; length of vertex 0.26; inter-ocular width 0.42-0.44; length of pronotum 0.44-0.45; width 0.88-0.94; length of tegmina 2.70-(2.727)-2.77, width 0.84-0.86 mm. ♀. Total length 3.48-(3.581)-3.65; width across eyes 0.97-1.04; length of vertex 0.28-0.33; inter-ocular width 0.46-0.50; length of pronotum 0.48-0.49; width 0.93-1.01; length of tegmina 2.77-(2.913)-2.99, width 0.84-0.91 mm.

The above description is based on a series of 3 males and 6 females from the Ak-Tash Mountains near Tashkent, Uzbekistan (-v.1923, *E. Smirnov*). *H. turanica* appears to be rather widely distributed in Central Asia, as it is known to occur in some other localities; it is a typically mesophilous, arboreal form.

H. (s.str.) anatolica sp. n.

♀. Quite similar to *turanica* in size, proportions and all other particulars except the shape of the subgenital plate, the lateral angles of which are broadly rounded, forming nearly semicircular lobes (fig. 45).

Measurements of the allotype: total length 3.54; width across eyes 0.99; length of

vertex 0.31; inter-ocular width 0.48; length of pronotum 0.48; width 0.97; length of tegmina 2.90; width 0.86 mm.

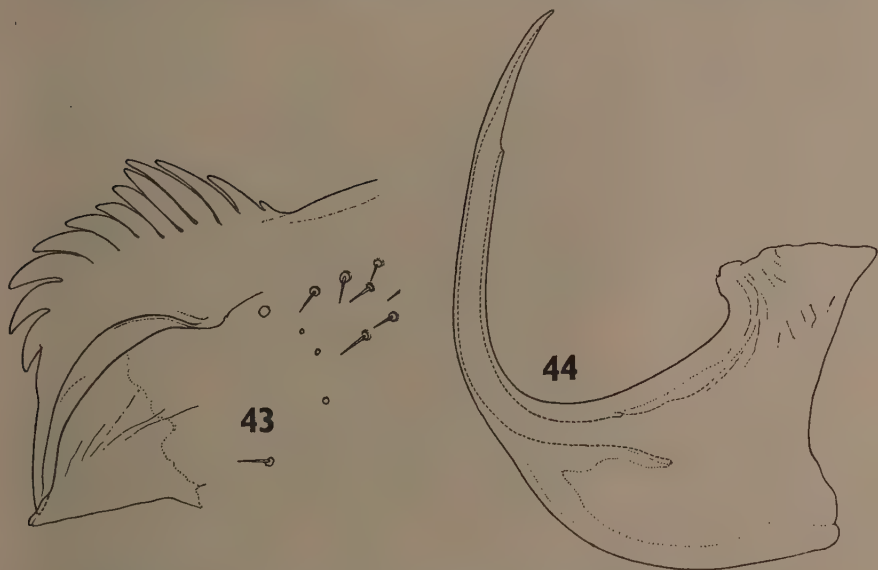
Described from a single female, taken in the neighbourhood of Ankara by Mr. Jenjouriste in December 1934.

The fourth species of *Hardya* s.str. occurring in the area here described is closely allied to the Tyrolian *H. signifera* (Then, 1896); that is:—

***H. (s.str.) sevanensis* sp. n.**

Easily distinguished from any other species by its diminutive size and rather robust stature.

♂. L/W ratio 2.89; tegminal index 2.96. General colour dark, head ornamentation as in *signifera*. Genital plates (fig. 37) precisely as long as broad, fairly similar in shape to those of *tenuis*, i.e. subquadrate with posterior margin straight and forming almost a

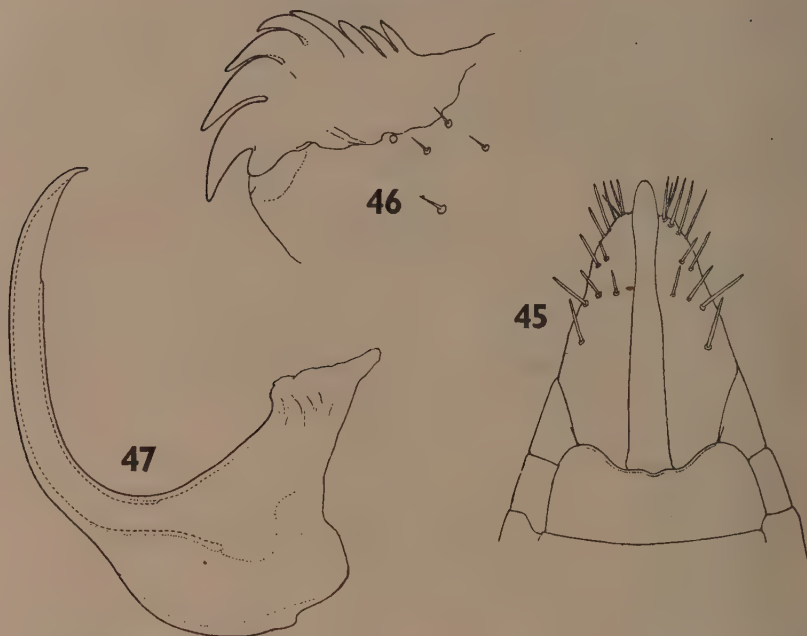


FIGS. 43-44.—*H. tenuis* (Germar) ♂, 43, comb of pygophor lobe; 44, aedeagus.

right angle with their short inner margin. Comb of the genital lobes (fig. 46) composed of only 8 teeth, of which the 4 proximal are slender and nearly straight and the 4 distal hook-shaped and increasing in size towards the apex of the lobe. Styles (fig. 41) somewhat intermediate in form between those of *tenuis*, on the one hand, and those of species of the *iranicola* group, on the other; relatively very slender. A similarly intermediate condition is exhibited by the aedeagus too, the apex of which is curved as in *iranicola*, but has its posterior wall only feebly thickened (fig. 47).

Measurements of the holotype: total length 2.29; width across eyes 0.79; length of vertex 0.22; inter-ocular width 0.35; length of pronotum 0.35; width 0.70; length of tegmina 1.89; width 0.64 mm.

One male from Elenovka at Sevan lake, S.S.R. of Armenia.



Figs. 45-47.—45, *H. anatolica* sp. n., ♀ subgenital plate; 46, *H. sevanensis* sp. n., comb of pygophor lobe; 47, aedeagus.

2. *Mimohardya* subgen. n.

Type of the subgenus, *H. (M.) heptneri* sp. n.

General appearance and proportions as in *Hardya* species of the *tenuis* group. First subapical cell of tegmina stalked, with its stalk usually very long. Ground colour dark brownish with black pigmentation strongly developed, some deep ferruginous markings on head and thorax and the usual light ornamentation extremely vivid, ivory-white intermixed with orange red.

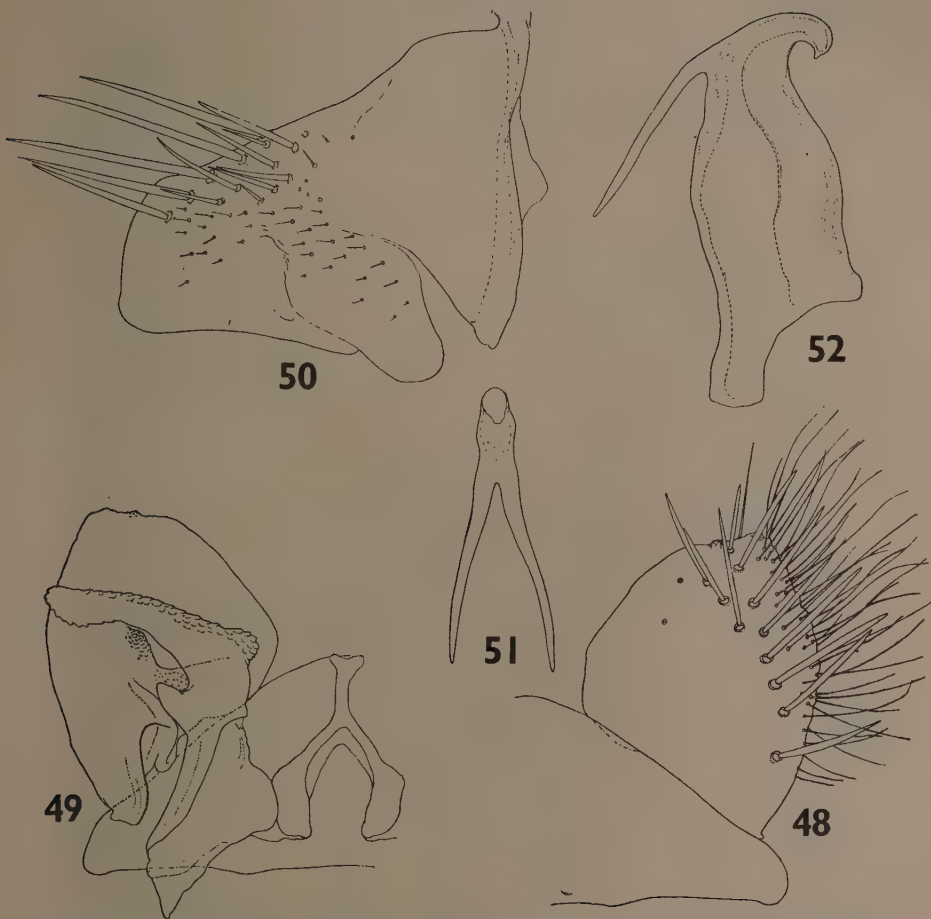
♂. Genital plates rather feebly sclerotised (entirely pallid), nearly obovate, with inner margins gradually diverging posteriorly and no traces of a subdivision into two lobes (figs. 48, 49). Lobes of the genital segment evenly sclerotised, simple, without any kind of special differentiation (fig. 50). Aedeagus (figs. 51-52) unusually robust, strongly compressed laterally, nearly straight, with two large acicular processes arising proximal to the gonopore and the apex strongly modified. Styles, too, of a quite unusual shape (fig. 49).

Hardya (Mimohardya) heptneri sp. n.

A small, rather slender species.

♂♀. L/W ratio ranging in the two sexes from 3.50 to about 3.65; tegminal index of male 3.47-3.50, of female 3.29-3.40. Vertex less than two-thirds (62 to 65 per cent.) of the pronotum in middle and of the inter-ocular space. Pronotum almost twice as broad as long in middle.

Measurements. ♂. Total length 3.05-3.10; width across eyes 0.84-0.88; length of vertex 0.26; inter-ocular width 0.40-0.42; length of pronotum 0.40-0.41; width 0.79-0.84;



FIGS. 48-52.—*Hardya* (*Mimohardya*) *heptneri* sp. n. ♂. 48, Genital plate, ventral view; 49, style and genital plate, dorsal view; 50, lobe of pygophor; 51, aedeagus, lateral view; 52, ventral view.

length of tegmina 2.51-2.55; width 0.72 mm. ♀. Total length 3.21-3.55; width across eyes 0.88-0.94; length of vertex 0.26-0.29; inter-ocular width 0.44-0.46; length of pronotum 0.40-0.44; width 0.85-0.89; length of tegmina 2.68-2.74; width 0.79-0.83 mm.

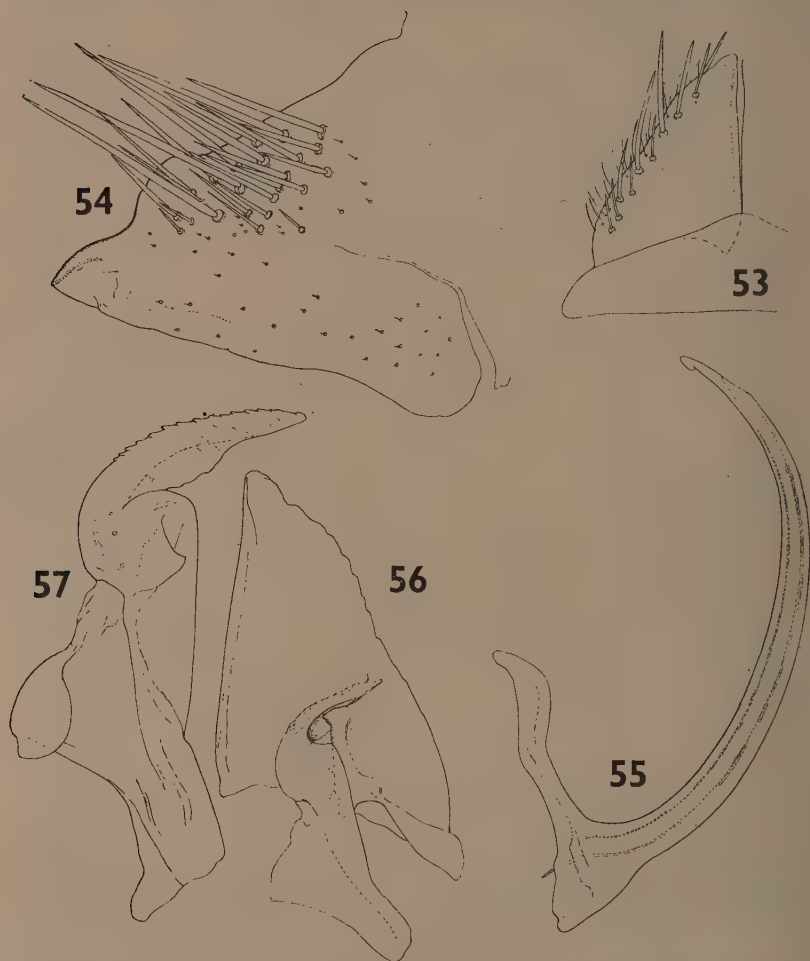
Described from 3 males and 4 females, collected in the vicinities of Kushka (Southern Turkmenia) by my friend, Professor W. G. Heptner, to whom the species is dedicated.

3. *Eohardya* subgen. n.

Type of the subgenus, *H. (E.) mira* sp. n.

Fairly robust species with L/W ratio 3.4 or less and tegminal index about 3.0. Vertex relatively very long, its median length being always more than two-thirds of that of pronotum

and subequal to (δ) or at least three-fourths of (φ) the inter-ocular space. First subapical cell of tegmina parallel-sided or but feebly narrowed towards its end, never lanceolate nor stalked; apical cells comparatively short and broad. Coloration nearly as in *Hardya* s.str. as regards its general tone, but of an obviously more variegated appearance, due to the greater intensity of the white markings on tegmina and the presence on the latter of a very



FIGS. 53-57.—*Hardya (Eohardya) mira* sp. n. ♂. 53, Genital plate; 54, lobe of the pygophor; 55, aedeagus; 56, style and genital plate, dorsal view; 57, style isolated, ventral view.

sharply contrasted subquadrate black spot at end of the inner subapical cell. Female subgenital plate yellowish with two dark spots at hind margin. Male genitalia of a quite generalised type not found to occur in any other group of *Hardya*-like JASSIDAE; viz., with genital plates forming together an isosceles triangle and having their inner margins contiguous throughout their length (fig. 53), and lobes of the genital segment without a

comb and rather evenly sclerotised (fig. 54). Aedeagus (judging from *mira* solely) unusually slender (fig. 55). Posterior portion of styles (figs. 56-57) sharply curved sideways, with dorsal edge broadly lamellate.

Eohardya apparently includes two previously described species, *H. imitata* (Haupt, 1921) from Sicily, and *H. fraudulenta* (Horváth, 1903) from Serbia and Hungary, and the following two new ones:—

Hardya (Eohardya) mira sp. n.

♂. General coloration rather dark. Vertex (fig. 58) with its lyriform figure distinctly narrower than in other species of *Eohardya* and much more narrowly rounded anteriorly, and with apical triangles fused together with the subapical ones to form a pair of rather large, oblique submarginal spots. Dark ornamentation of face (fig. 59) precisely as in the male of *imitata* (according to Haupt's fig. 4, which is undoubtedly drawn from a male of that species), except that the subocellar spots are apparently somewhat smaller. Tegmina with their dark pattern strongly developed, the apical cells being almost entirely filled up with fuscous (fig. 60). L/W ratio 3.38; tegminal index 3.08. Vertex about four-fifths as long in middle as pronotum and distinctly shorter than wide between bases of eyes. Pronotum more than twice as broad as long in middle (39:17). Genitalia as figured.

Measurements of the holotype: total length 2.90; width across eyes 0.86; length of vertex 0.31; inter-ocular width 0.35; length of pronotum 0.37, width 0.84; length of tegmina 2.31, width 0.75 mm.

Described from a single male from Zergendeh, N.W. Persia (7.xii.1936).

Hardya (Eohardya) byzantina sp. n.

♀. General coloration comparatively light. Lyriform figure of vertex (fig. 61) as in *H. imitata*, i.e. rather broad and obtusely rounded anteriorly; supra-antennal spot large; dark ornamentation of face (fig. 62) moderately developed, leaving rather large areas of the base colour uncovered. Pronotum lacking the anterior dark spots found in *H. imitata*. Tegmina with their dark pattern relatively feebly developed, the distal spot of the inner subapical cell being of a much deeper tint than the rest of its elements. Subgenital plate of the ground colour (light ochreous), posteriorly with a roundish fuscous spot each side of middle and the lateral margins distinctly infusate.

L/W ratio 3.23-3.24. Vertex in middle 73 to 88 per cent. of the median length of pronotum and of the inter-ocular space, which are usually subequal in size; pronotum precisely twice to $2\frac{1}{2}$ times as broad as long in middle; tegminal index 3.01-3.03.

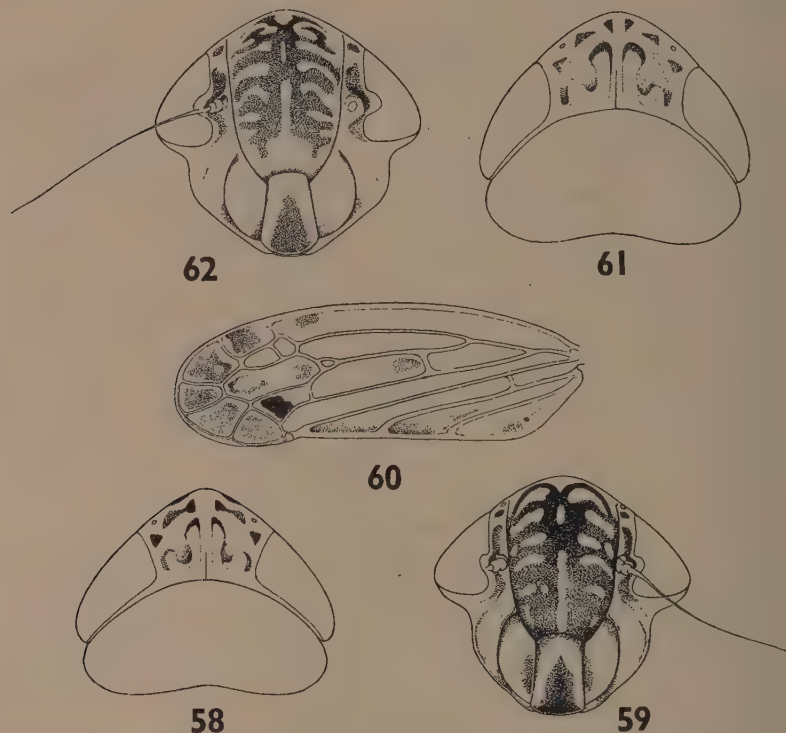
Measurements. Total length 2.99-3.12; width across eyes 0.92-0.97; length of vertex 0.32-0.35; inter-ocular width 0.40-0.44; length of pronotum 0.40-0.46; width 0.88-0.92; length of tegmina 2.33-2.44, width 0.78-0.80 mm.

Three females (one allotype and two paratypes) from Bujuk-Dere near Istanbul.

H. byzantina is evidently very similar to *H. imitata* Haupt, with which it closely agrees in all features except its much smaller size (*imitata* being, according to Haupt, 4 mm. long); moreover, it seems to be somewhat lighter than the last-named species and to exhibit some minor differences in the details of the pigmentation.

It is worth noting that my previous record of *imitata* from Italy (1933, *Boll. Soc. ent. Ital.* 12: 270) is based on a female, extremely similar to the above described specimens from Turkey in size, coloration and most of the proportions,

and distinguished from them only in its slightly shorter vertex (68 per cent. of the median length of pronotum) and somewhat more slender general form (the L/W ratio being 3.30). This example may apparently be conspecific with *byzantina* rather than with *imitata*, if Haupt's data on the dimensions of the latter are correct.

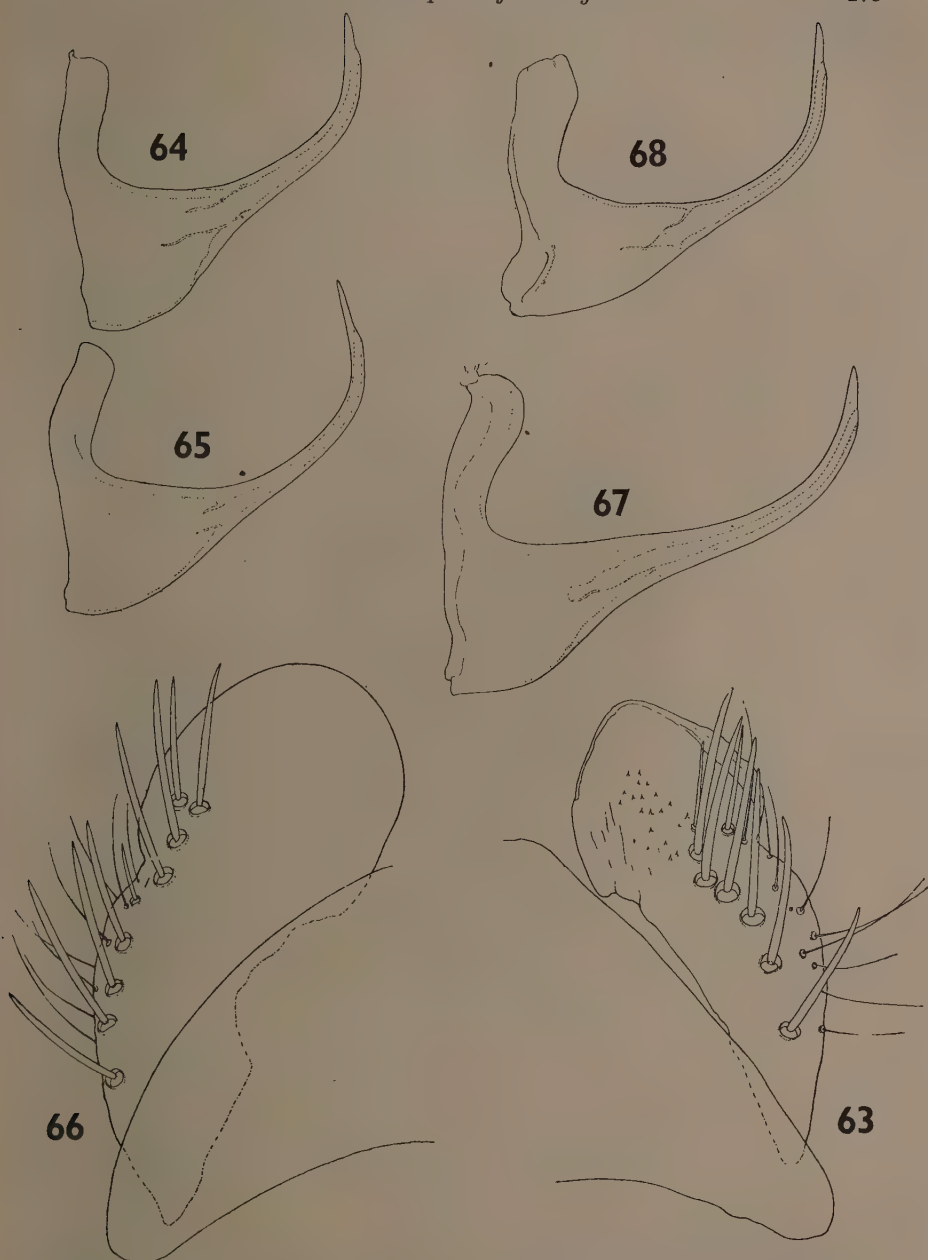


FIGS. 58-62.—*Hardya* (*Eohardya*) *mira* sp. n. ♂. 58, Head and pronotum; 59, face; 60, tegmen. *H. (E.) byzantina* sp. n. ♀, 61, head and pronotum; 62, face.

VII. Three new species of the genus *Stenometopiellus* Haupt. 1917 (figs. 63-68).
Fam. EUSCELIDAE.

The genus *Stenometopiellus* was established by Haupt in 1917 (*Wien. Ent. Ztg.* 36 : 250) for a single new species, *S. sigillatus* Haupt from Kerki, Eastern Turcomenia; as no further data on this genus have thus far appeared, it is considered as monotypical and of purely Turanian distribution. My recent studies on the subject show, however, that this is not the case, and that *Stenometopiellus* occurs in a great number of hitherto undescribed species over the Steppe and a part of the Desert zones, from Asia Minor to Dzhungaria and Northern Mongolia.

The Anatolian representative of this genus proves to be closely allied to its most typical, slender and long-winged species, centring about *S. sigillatus*



FIGS. 63-68.—*Stenometopiellus angorensis* sp. n. ♂, 63, genital and subgenital plates; 64, aedeagus. 65, *S. iranicus* sp. n., aedeagus. *S. sigillatus* Hpt. ♂, 66, genital and subgenital plates (neighbourhood of Tashkent); 67, aedeagus. 68, *S. araxis* sp. n., aedeagus (Kamerlu, Armenia).

Haupt, 1917, and definitely deserticolous in their ecological requirements. It may be shortly characterised as follows:—

***Stenometopiellus angorensis* sp. n.**

Similar in general appearance, main proportions, and type of coloration to the Turkessian *S. sigillatus*, but much smaller, with dark pigmentation (in hibernating specimens) much more developed than is usually the case in the last-named species, and with male genitalia rather distinct.

L/W ratio of male 3.77, of female 3.70 to nearly 4.0 (average 3.82); tegminal index of the former 3.83, of the latter 3.53–3.83 (average 3.67). Male genital plates of a rather irregular shape (fig. 63), with exterior margin broadly membranaceous and inner margin prominently angulated at base; aedeagus (fig. 64) distinctly shorter than in *sigillatus*, much more arched and more strongly reflexed apically, and with terminal process somewhat less robust.

Measurements. ♂ (Holotype): total length 2.84; width across eyes 0.75; length of vertex 0.25; inter-ocular width 0.31; length of pronotum 0.35; width 0.34; length of tegmina 2.31; width about 0.60 mm. ♀ (Allotype and paratypes): total length 3.04–3.17; width across eyes 0.77–0.84; length of vertex 0.25–0.27; inter-ocular width 0.35–0.38; length of pronotum 0.40, width 0.72–0.79; length of tegmina 2.52–2.62; width 0.68–0.75 mm.

Described from a series of 1 male and 6 females collected by Mr. Jenjouriste in the neighbourhood of Ankara, in December 1934.

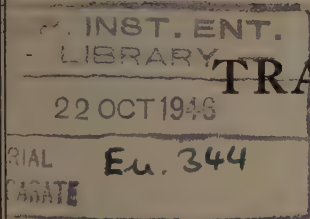
The principal difference between *S. angorensis* and its nearest relatives are summarised in the following key:—

- 1 (2). Total length of male about 3.40 mm.; its L/W ratio 4.16 and tegminal index nearly 4.25. Vertex rather acutely angled. Distal part of aedeagus (fig. 65) very slender and strongly arched; its terminal process nearly acicular, more than six times as long as wide at base (in a lateral view). N.W. Persia: Zergendeh. ***S. iranicus* sp. n.**
- 2 (1). Smaller and distinctly less slender species with L/W ratio and tegminal index not over 4.0; vertex more bluntly angled, aedeagus not as above.
- 3 (4). Total length of male 3.20–3.25, of female 3.30–3.56 mm. Distal portion of male genital plates nearly round (fig. 67). Aedeagus (fig. 66) rather feebly curved distally, with terminal process comparatively stout (about three times as long as wide at its base). Turcmenia, Uzbekistan, Tadzhikistan; widely spread all over the area of its host-plant, *Poa bulbosa vivipara*. ***S. sigillatus* Haupt.**
- 4 (3). Total length of male less than 3.10, of female 3.04–3.40 mm.; distal portion of the male genital plates narrower, distinctly angulated; aedeagus distally more strongly arched.
- 5 (6). Smaller: total length of male about 2.85; of female 3.03–3.17. Distal part of aedeagus (fig. 64) comparatively thick, its terminal process about three times as long as broad at base. Asia Minor: Ankara. ***S. angorensis* sp. n.**
- 6 (5). Larger: total length of male 2.90–3.08, of female 3.25–3.40 mm. Distal part of aedeagus (fig. 68) decidedly more slender, its terminal process nearly four times as long as broad at base (fig. 68). Deserts and semi-deserts of Soviet Armenia and Azerbeidzhan within the limits of distribution of the *Poa bulbosa*-formation. ***S. araxis* sp. n.**

As two of the closest allies of *S. angorensis* are ecologically rigorously confined to the same host-plant, the highly peculiar ephemeroïd perennial grass—*Poa bulbosa vivipara*—I think it probable that *S. angorensis* will also prove to live on this grass.

Vol. 97. Part 7. Pp. 177-186, 2 figs.

21st October, 1946.



THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

X SOMEREN, E. C. C. van. Ethiopian CULICIDAE.	PAGE
Tribe Megarhinini—notes and descriptions	177-186, 2 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 2s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D. }

A. WELTY, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,
D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939.

Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

ETHIOPIAN CULICIDAE. TRIBE MEGARHININI—NOTES AND DESCRIPTIONS

By E. C. C. van SOMEREN.

(Section of Medical Entomology, Medical Research Laboratory, Nairobi, Kenya.)

Manuscript received 29th October, 1945.

(Read 5th June, 1946.)

WITH TWO TEXT-FIGURES.

It is convenient to divide the African *Megarhinus* Robineau-Desvoidy into two main groups and the *M. brevipalpis* Theobald and *M. lutescens* Theobald groups used here are as defined by Edwards (1941).

On examining a collection of *Megarhinus* from Kenya and Uganda, a considerable amount of colour variation was noted among the individual adults of the various species. In consequence Edwards' (1941) key was found to be inadequate for the determination of the species of the *brevipalpis* group.

The variations noted are given below under the species headings, and descriptions of the larvae and pupae are given where the early stages have not been described before. Two new species of the *lutescens* group are described and also the females of *M. lutescens* Theobald and *M. barbipes* Edwards.

A revised key, largely following that of Edwards, has been compiled to include the two new species and using, in the author's opinion, more reliable characters for the differentiation of the *brevipalpis* group.

M. brevipalpis group.

Edwards (1941) describes *M. barbipes* from one male specimen from the Mpanga Forest, Toro, Uganda, and suggests that it may perhaps be a local form of *M. phytophagus* Theobald. As I have not been able to compare *M. barbipes* with *M. phytophagus* and as the female specimens of *M. barbipes* from the Kaimosi Forest, Kenya, and Bwamba, Toro, Uganda, differ slightly from the description of *M. phytophagus* given by Theobald (1910) and Edwards (1941), I am retaining the specific status given to *M. barbipes* by Edwards. *M. barbipes* will, however, probably prove to be a subspecies of *M. phytophagus*.

The Kaimosi material was compared with three specimens of *M. barbipes* from Bwamba, Toro, Uganda, which is near enough the type locality of *M. barbipes* to make the identification of the Bwamba specimens fairly accurate.

While endeavouring to determine the imagines of this group Edwards key proved to be unsatisfactory, owing to the use, in sections 3 and 4, of characters which have proved to be variable. Thus, at section 3, the only differentiating character given for females or damaged males, when the hind tarsi are either missing or rubbed, is the colour of the abdomen. This character proved very unreliable as *M. brevipalpis* Theobald and subsp. *conradti* Grunberg, which usually have blue or green scaled tergites, may occasionally be either, "blue shading to violet" (*brevipalpis*, Edwards, 1941), or mainly purple (*conradti*, Edwards, 1941). Thus on the colour of the abdomen they could be run down to *M. phytophagus* or *M. barbipes* in Edwards' key.

M. barbipes, on the other hand, has proved to have considerably more blue on the tergites than is allowed by Edwards. It is therefore very often extraordinarily difficult to decide whether the abdomen of a specimen examined should be considered largely blue or purple scaled above.

At section 4 of his key Edwards uses the colour of the supra-alar bristles as one of the differentiating characters for *M. brevipalpis* and subsp. *conradti*. This character has also proved to be unreliable, as on examining a large series of *M. brevipalpis* the colour of the supra-alar bristles was found to vary from bright gold through dark brown to black.

The use of these two characters impaired the efficacy of Edwards' key, and more reliable characters had to be found to differentiate the species.

The male terminalia of *M. brevipalpis* subsp. *conradti*, and *M. barbipes* were all of the usual *brevipalpis* group form and showed no diagnostic characters.

A useful character for differentiating the males of *M. brevipalpis* subsp. *conradti*, and *M. barbipes*, in the event of missing or rubbed hind tarsi, was found in the vestiture of the palpi, viz. the length of the bristles on the penultimate segment. The amount of white on the fifth sternite also proved useful for differentiating the males of *M. brevipalpis* and subsp. *conradti* from *M. barbipes*.

The fifth sternite of *M. barbipes* is extensively dark, and most specimens have only a narrow line of white scales on the distal edge of the segment, but occasionally small apical lateral white patches are present. The fifth sternite of *M. brevipalpis* and subsp. *conradti*, however, has a large patch of white scales, which may or may not be interrupted in the middle.

The females are easily distinguished by the amount of white on the tarsi and by the colour of the lateral tufts of the sixth tergite.

As the tufts of the sixth tergite are the same in both sexes, section 3 of Edwards' key has been changed to make use of this character, thus grouping *M. brevipalpis* with *M. barbipes* (tufts of sixth tergite white) and *M. brevipalpis* subsp. *conradti* with *M. phytophagus* (tufts of sixth tergite mainly black). This grouping gave an opportunity to use some of the differentiating characters noted above.

Unfortunately no specimens of *M. phytophagus* were examined and the vestiture of the penultimate segment of the male palpi is not known. An alternative character to the vestiture of the male hind tarsi is the amount of white on the fifth abdominal sternite, but with the existing description of *M. phytophagus*, based on three females and one male, it is not possible to tell if this is a constant character.

Megarhinus brevipalpis Theobald.

Adult female.—On the whole the *M. brevipalpis* examined agreed with the description given by Edwards (1941) but a certain amount of variation occurred. The supra-alar and scutellar bristles were found to vary from golden to dark brown and black. The fourth tergite sometimes has lateral patches of pale scales which have a whitish gloss, or has definite basal lateral patches of white scales as on the other tergites. This character is also noted by Edwards, under variations, for subsp. *conradti*. The large white patch on the fifth sternite is not always interrupted in the middle.

Male.—More often with a few black hairs at the apex of the sixth abdominal tergite and often with two lateral patches of white scales on the seventh sternite; fifth sternite of all specimens examined with the white patch interrupted in the middle. Penultimate

segment of palpi with a few very short bristles on the inner and outer surfaces, those on the outer surface about the same length as those on the inner surface.

Pupa as described by Edwards.

Larva.—Indistinguishable from that of *M. brevipalpis* subsp. *conradti* as described by Macfie and Ingram (1922) and Hopkins (1936).

Head, lateral setae of abdomen and thorax, siphon, and anal segment as in subsp. *conradti*. Subventral tuft with 3–5 branches. Lower caudal setae with 3–5 branches and upper with 4–6 branches. Ventral brush composed of 8–9 pairs of single, strong, coarsely plumose setae. Gills short and rounded.

Specimens examined from KENYA: Nairobi, 2 males and 2 larval pelts; Mombasa, 7 males and 15 females (*van Someren and de Boer*), 4 males (*Symes and Hopkins*), and 4 males and 6 females and 2 larval pelts and 2 pupal pelts (*Teesdale*); Kaimosi Forest, 4 males and 9 females and a few larval and pupal pelts (*Garnham, Harper, and Highton*); Kisii, 1 female; Kitale, 1 female.

Subsp. *conradti* Grunberg.

Female.—All the supra-alar bristles of the specimens examined were black but in one specimen the scutellar bristles were bright golden. The colour of the abdominal tergites 4–7 of the majority of the specimens from Bwamba was a dullish purple as found in *M. barbipes* and mentioned under variations by Edwards (1941). A few specimens had brilliant metallic green scales on the tergites shading to blue towards the apex of the abdomen.

Male.—Vestiture of penultimate segment of palpi as in *M. brevipalpis* but bristles on outer surface slightly longer, but not more than $1\frac{1}{2}$ times the length of those on the inner surface. White patch on fifth abdominal sternite occasionally interrupted in the middle.

Specimens examined from UGANDA: Bwamba, Toro, 19 males and 9 females (*Harper*).

Megarhinus barbipes Edwards.

The larva, pupa, and adult female are described below and a few additional notes are given on the male.

The adult female of *M. barbipes* differs from *M. phytophagus* female by having more extensive white markings on the tarsi and by having the lateral hairs on the sixth tergite all white; black hairs, if present, very few and confined to extreme apex of segment.

Female.—*Head*. Flat scales metallic green, shading to dark blue between the eyes; round the eye margins there is sometimes a paler line which has a dull purple sheen. Tori black, with a few small flat white scales on the inner borders; first flagellar segment of antennae with a patch of small black scales above. Palpi and proboscis dark with blue or purple sheens. *Thorax*. Metallic blue-green scales on scutum dorsally, sometimes brassy scales on anterior border of scutum and scutellum, and scales on lateral borders lighter green with dull yellowish or mauve reflections. Scales on *apn* and *ppn* blue but a few white scales present. Pleural scales all white. Supra-alar and scutellar bristles usually golden, sometimes dark brown, and occasionally black. *Abdomen*. Tergite 1 green; 2–3 purple, usually with a patch or median line of blue scales, or sometimes all blue; 4–7 dull purple. White lateral patches on all tergites. Long lateral hairs on sixth tergite all white, very occasionally with a few black hairs at the apex, lateral hairs on seventh tergite black, and orange on eighth tergite. Sternites dark, 2–3 with large white lateral patches, 4 all dark, 5 very often nearly all white or with a large white patch which is sometimes narrowly interrupted in the middle, 6 with white lateral borders, and 7 sometimes all dark or with lateral white patches.

Legs blue or purple and sometimes green on tibiae. Femora white below and tibiae all dark. Tarsi dark with white rings. Fore tarsi: first segment sometimes all dark, occasionally with an indistinct pale blue area at the base, but usually there is a small basal white band or patch of white scales above which does not extend over a $\frac{1}{4}$; second segment all white; third sometimes all white, but usually white with a narrow black band at the apex, and sometimes all white above and narrowly black below; fourth with a few white scales at the base; fifth all black or with a few white scales at the base. Mid tarsi: first segment with a broad white ring at the base, extending to about a $\frac{1}{4}$ above, and may be extended in a narrow line below to a $\frac{1}{2}$; second and third all white; fourth all white above and narrowly black below for its full length, or only on apical $\frac{1}{2}$, or white all round; fifth broadly or narrowly white at the base above. Hind tarsi: first segment with a broad white basal band, which may be interrupted below, and which extends to about a $\frac{1}{4}$; second white with a narrow black ring at the apex; third with or without a white line on basal $\frac{1}{2}$ of posterior surface; segments 4-5 all dark. *Wing* scales blue. There is sometimes a small area of brassy scales at the base of the costa below.

Male the same as the female and as described by Edwards (1941). *Head*. Penultimate segment of palpi with a number of hairs on the inner and outer surfaces, those on the outer surface conspicuously longer than, some of them at least twice the length of, the hairs on the inner surface. *Abdomen* more often with a few black hairs laterally on sixth tergite. Sternites 2-3 usually all dark, white patches if present confined to small basal lateral patches, fourth all dark, fifth usually with a narrow uninterrupted line of white scales on distal edge of segment and sometimes expanding laterally to form small triangular patches, sixth with broad white lateral borders, seventh sometimes all dark but most often with broad lateral white borders. *Legs*. Fore tarsi all dark. Mid tarsi: first segment with a small white patch below; second white below on the basal $\frac{1}{2}$ or more; 3-5 all dark. Hind tarsi: first segment with a small white patch on the posterior surface at the base; second white below on the basal $\frac{1}{2}$ or all white below; 3-5 all dark.

Pupa.—Indistinguishable from *M. brevipalpis* Theobald.

Larva.—Indistinguishable from *M. brevipalpis* Theobald. Head, siphon, anal segment, and lateral setae of thorax and abdomen as in *M. brevipalpis*. Siphonal index 2; sub-ventral tuft with 3-6 branches. Lower caudal setae with 3-4 branches and upper with 4-6 branches. Ventral brush composed of 7-9 pairs single, stout, coarsely plumose setae.

Specimens examined from UGANDA: Bwamba, Toro, 2 males (*Harper*), 1 female (*Haddow*). KENYA: Kaimosi Forest, North Kavirondo, 51 males, 68 females, many larval pelts, and a few pupal pelts (*Garnham*, *Harper*, and *Highton*); Kakamega, North Kavirondo, 1 male and 2 females (*Garnham*, *Harper*, and *Highton*).

Some of the Kaimosi larvae, pupae, and adults will be deposited in the British Museum (Nat. Hist.).

M. lutescens group.

Edwards (1941) includes four species within this group, *M. lutescens* Theobald, *M. erythrurus* Edwards, *M. viridibasis* Edwards, and *M. aeneus* Evans. The paucity of material available for study made it impossible to state the exact status of *M. erythrurus*, *M. viridibasis*, and *M. aeneus*, and Edwards provisionally accorded specific status to all.

The new member of this group, to be described in this paper as *M. kaimosi* sp. n., is very similar in general colour and form of male terminalia to *M. erythrurus* and should probably be considered a subspecies of it, but owing to the uncertain status of *M. erythrurus*, *M. viridibasis*, and *M. aeneus* it was considered best to follow Edwards and accord *M. kaimosi* sp. n. specific status,

pending such time as more material of the Nigeria forms is available for examination.

Another new species *M. nairobiensis* sp. n., described below, is given specific status as the structure of the ninth tergite of the male terminalia and the vestiture of the male palpi together with the median line of dark purple scales on the sternites are considered specific characters by which to separate this species from *M. lutescens* and *M. viridibasis*.

The known larvae and pupae of this group can be separated from those of the *brevipalpis* group but it is not possible to separate the species of either group.

The larvae of the *lutescens* group are easily distinguished by the number of branches (1-3) of the subventral tuft and by the lateral setae of the abdomen and the grouping of the long and short spines on the distal edge of the saddle.

The pupae differ from the *brevipalpis* group by the length of seta S on the first abdominal tergite and by the length of seta A on tergites II-VI.

Megarhinus lutescens Theobald.

The female, one very damaged specimen with the hind legs and mid tarsi missing, agrees with the description given of the male by Edwards (1941). A few additional characters, noted in both male and female, are given below.

Adult female.—*Head*. Palpi with greenish metallic scales at bases of segments above; scales at apices of segments with blue, purple, or whitish reflections. Proboscis dark. Tori black, covered with a grey bloom, and with a few short, fine, pale hairs, on inner borders; first flagellar segment of antennae with a patch of small dark scales above. *Thorax*. In some lights the scutal scales have a metallic green sheen dorsally but scales on lateral borders golden. Scales on *apn* mainly golden but some of the gold scales have a purplish gloss. *Abdomen* as in the male but the seventh tergite has bright purple scales. Lateral tufts of tergites 6-8 golden and very short, but this may be due to rubbing. *Legs*. Fore and mid femora and tibiae as in the male. Fore tarsi dark, without white rings; mid tarsi with a broad white band at the base of the first segment; segments 2-5 missing. Hind legs missing. *Wings* with bright blue-green scales shading to yellow at the base of the costa.

Male.—*Head*. Dark scales of tuft on first flagellar segment of antennae with pale blue and whitish reflections. *Thorax*. Scutal scales dull brown but with yellow-green metallic sheens in some lights. *Abdomen*. Seventh tergite clothed with bright purple scales. *Terminalia*: lateral groups of hairs on ninth tergite stout and with about 16 hairs in each group.

One male and one female from Mombasa (*Teesdale*). The female, from which the above description was compiled, will be deposited in the British Museum (Nat. Hist.).

Megarhinus nairobiensis sp. n.

This species is nearest to *M. lutescens* Theobald, but differs in the structure of the ninth tergite of the male terminalia and the vestiture of the male palpi, and in both sexes by having bristles on the sternopleurae and two long fine bristles on the lower mesepimeron and by having a bright purple gloss on the abdominal tergites and a median longitudinal line of purple scales on the sternites.

Adult female.—*Head*. Light metallic green scales above, golden laterally, and blue scales round eye margins. Tori dark, covered with a frosty grey dusting, and without scales; first flagellar segment of antennae with a tuft of black scales above. Palpi with

brassy scales below; scales on upper surface mainly metallic blue but with a patch of purple scales at the tip and another about the middle. Proboscis brassy below on basal $\frac{1}{2}$, remainder black with a coppery sheen. *Thorax*. Metallic blue-green scales on scutum. A large patch of silvery white scales in the middle of the pleurae, scales above and below golden; *apn* with blue and golden metallic scales, the gold scales sometimes with a purple gloss; *ppn* with golden scales. Sternopleurae with a patch of long hairs in the middle; lower mesepimeron with 2-3 long bristles. Coxal scales all golden. *Abdomen*. Mainly purple above and golden below. First tergite with metallic green scales and a few purple ones at the apex of the segment, tergites 2-7 coppery with a strong purple gloss, and eighth



FIG. 1.—Larva of *M. nairobiensis* sp. n. Lateral setae of abdomen.

tergite golden with a purple gloss. All tergites with broad, bright golden, lateral borders. Sternites golden and with a narrow median longitudinal stripe of purple scales on segments 2-6 and a large triangular patch of purple scales on the seventh segment. Lateral bristles on tergites 7-8 scanty and golden. *Legs* blue shading to purple with a few scattered metallic green and coppery scales, especially on the femora. Anterior surfaces of all femora golden below to near the tip which is dark all round. On the fore femora the golden scales tend to have a greenish sheen towards the tip. Posterior surfaces of femora golden on basal one-third and below to near the tip. All tibiae dark, with a narrow pale greenish stripe below which is more noticeable on the hind tibiae. Fore tarsi without bands; mid tarsi with a small inconspicuous patch of white scales on the outside near the base of the first segment, second segment nearly all white above, only narrowly dark at the base and apex, segments 3-5 all dark; hind tarsi with a small patch of white scales below near the base of the first

segment, second segment dark, third white all round on a little more than the basal $\frac{1}{2}$, segments 4-5 all dark. *Wing* scales blue-green, with a patch of bright blue scales at the base of the first vein, and a purple area involving the costa and the first vein at the apex of the wing. A patch of golden scales is present on the costa and subcosta at the base below.

Male.—Essentially the same as the female. *Head*. The first flagellar segment of the antennae has, on the upper surface, a large patch of dark scales which have blue or purple reflections. Palpi dark above with a brassy sheen basally and a blue or purple sheen apically; shaft and penultimate segments mostly golden below but with the tips of all segments dark all round. Penultimate segment with 5 long hairs below and 4 short stout bristles above. *Abdomen* with sternite eight nearly all dark. *Legs* without any white patches on mid tarsi. *Terminalia*. Style not greatly enlarged in the middle, middle third

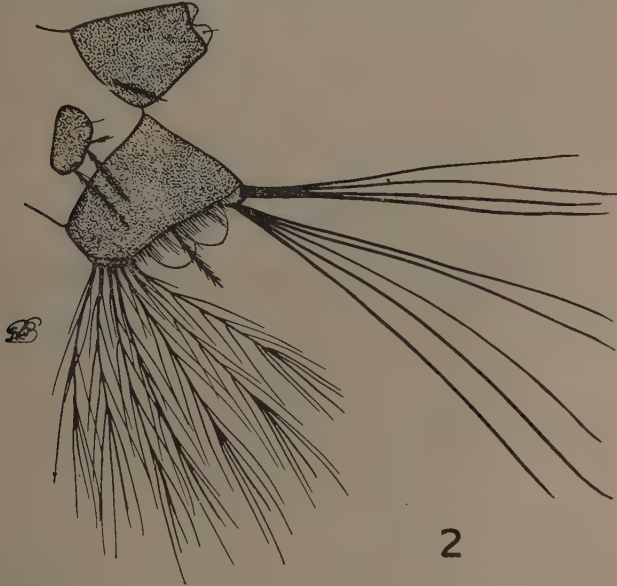


FIG. 2.—*M. nairobiensis* sp. n. Terminal segments of larva.

only $1\frac{1}{2}$ times as wide as the two ends. Tergite rather deeply emarginate in the middle and with lateral groups of about 23 long fine hairs.

Pupa lost.

Larva (fig. 2).—The larva is a clear purple colour when alive. *Head*. Antennae smooth, cylindrical, and less than $\frac{1}{2}$ the length of the head; tuft at about five-sixths and composed of 2-3 dendroid branches; sub-terminal seta a single, long, simple hair, about one-third the length of the antennae, and placed outside and a little below the tuft. Setae A, B, and C fine, simple, setae, all less than $\frac{1}{2}$ the length of the head, placed close together, and with their bases almost in a straight line. A is either a single seta or split beyond the base into 2-3 fine branches, B is split beyond the base into 3-6 branches, and C is a single seta; *d* is a single seta with 2 dendroid branches and placed out of alignment with, below, and inside C. Mentum with 7-8 coarse uneven teeth on either side of the central tooth; the central tooth long, followed on either side by one short tooth, followed by a large tooth which is a little longer than the central tooth, the following 3-4 teeth short, and the 2 basal teeth large. *Thorax*. Setae of thorax like those of the *brevipalpis* group but slightly shorter.

Abdomen. Lateral setae (fig. 1) differ from those of the *brevipalpis* group in that none of the setae of the lateral groups is stouter than the others. Siphon conical, heavily chitinated, and dark to tip; index $1\frac{1}{2}$ in crushed specimens. The subventral tuft, placed very near the base of the siphon, is usually a single, fairly stout, coarsely plumose seta, but in one specimen it is bifid on one side of the siphon. Saddle heavily chitinated and complete. The distal edge of the saddle is fringed with strong spines; on the upper and lower edges there is a group of alternating long and short spines but on either side of the lateral seta the short spines are irregularly spaced, dividing the long spines into patches of varying size, but usually a fairly large patch of long spines only, on either side of lateral seta. Lateral seta, placed on the distal edge of the saddle, is a single, stout, coarsely plumose seta, about $\frac{1}{2}$ the length of the saddle. Lower caudal seta with 3-5 branches; upper with 5-7 branches. Ventral brush composed of 7-8 pairs of single, long, coarsely plumose setae. Gills subequal, round, and about one-third the length of the saddle.

Collected by Mr. G. R. Cunningham van Someren from tree holes in the City Park, Nairobi, Kenya.

Described from 2 males, 2 females, and 3 larval pelts.

The types will be deposited in the British Museum (Nat. Hist.).

Megarhinus kaimosi sp. n.

This species is apparently very similar to *M. erythrurus* Edwards (ex description) but differs from *M. erythrurus* by having a dark median longitudinal line of purple scales on the sternites which are otherwise bright golden yellow.

Adult female.—*Head.* Flat scales on head metallic green with a narrow line of blue scales round the eye margins. Tori black, with a grey bloom, and without scales; first flagellar segment of antennae with a patch of small dark scales above. Palpi dark, with brassy or coppery sheens, and two patches of metallic blue or purple scales above, one at the apex and one about the middle. Proboscis dark. *Thorax.* Scutum covered with flat blue-green scales. Scales on *apn* blue; *ppn* with golden scales below and a narrow line of blue-green scales above. Pleurae with a large patch of white scales in the middle; lower sternopleurae and pre-alar area covered with golden scales which have a purple sheen. At least two bristles on the lower mesepimeron. Fore coxae golden with or without patches of golden scales which have a purple sheen; mid and hind coxae with a patch of white scales at the base of each, fore coxae all gold. *Abdomen.* Scales on first tergite blue or sometimes green; second tergite sometimes blue and sometimes green or purple with a patch or sprinkling of blue scales; tergites 3-7 all purple, sometimes 3 has a blue sheen; eighth tergite purple or golden. All tergites with narrow lateral borders of golden scales which have a purple sheen. Sternites golden, gold scales sometimes with a purple sheen, and a median longitudinal line of dark purple scales on segments 2-6; seventh segment with a broad triangular patch of purple scales. Lateral tufts of tergites 6-8 bright red. *Legs* dark, with purple and blue sheens. All femora dark above and golden below, fore femora only narrowly so towards the apex. Fore and mid tibiae all dark, hind tibiae with a patch of white or brassy scales below at two-thirds. Fore tarsi all dark. Mid tarsi: first segment with or without a white patch below at the base, the white patch sometimes extends on to the upper surface to form an ill-defined, narrow, white ring, which is slightly removed from the base of the segment; second segment with a white patch below on the basal $\frac{1}{2}$ or all white below; here again the white scales may extend on to the upper surface. Hind tarsi: first segment with a white patch below near the base; third segment white below on the basal two-thirds. *Wing* scales blue and sometimes a small patch of brassy scales below at the base of the costa.

Male.—Essentially the same as the female. *Head.* Palpi dark above, with a pale bluish area at apex and about the middle of the shaft another pale bluish area which extends towards the base; golden below with narrow dark rings at the base, middle, and apex. Penultimate segment dark above and golden below with a narrow dark ring at the base and a broader one at the apex; 11–15 short hairs above and 9–12 longer hairs below. Ultimate segment all dark. *Abdomen.* Same as in the female but the golden scales of the sternites sometimes have a more pronounced purple sheen. The median longitudinal stripe of dark purple scales on sternites 2–5 is sometimes broader than in the female and narrower on 6–7; the triangular patch on the seventh sternite is sometimes reduced to a narrow median line. Lateral hairs of tergites 6–8 long and bright red, forming conspicuous bright red caudal tufts. *Legs* as in the female. White markings on under surfaces of tarsi very variable, sometimes extending on to upper surfaces to form narrow or broad, ill-defined, white bands, but usually at least a narrow dark stripe the full length of the tarsal segment above. *Terminalia.* Middle third of style enlarged, about twice the width of the two ends; ninth tergite not very deeply emarginate and with 26–29 hairs in each lateral group.

Pupa.—Indistinguishable from *M. erythrurus* as described by Edwards (1941). Additional characters noted are as follows:—all setae sparsely and finely plumose. Dorsal seta fairly long and placed well behind the trumpets. Setae O, P, and R single or sometimes split distally into 2–3 branches; O and R about one-third the length of P. Float hair not such a large tuft as in the *brevipalpis* group; fewer branches and not so dendritic. K 8–9 times the length of H. L and M very short, about equal in length to H, single or with 2–3 branches. Tergite II: B single and about the length of the preceding segment, C single or with 2–3 branches and shorter or equal in length to B. Tergites III–V: C single and the same length as, or shorter than, B. Tergite VIII: A stouter than on the preceding segment and about one-seventh the length of the paddles. Paddles pale and square ended; fringe reaching to $\frac{1}{4}$ on external margin.

Larva.—Indistinguishable from *M. nairobiensis* sp. n. Head, siphon, saddle, and setae of abdomen and thorax, as in *M. nairobiensis*. Subventral tuft a single, stout, coarsely plumose seta, or divided into 2–3 branches beyond a $\frac{1}{4}$. Lower caudal seta with 5–6 branches; upper with 6–9 branches. Ventral brush composed of 8–9 pairs, long, single, coarsely plumose setae.

Collected by Dr. Garnham, Mr. Harper, and Mr. Highton, Medical Department, Kenya, from the Kaimosi Forest, North Kavirondo, Kenya.

Described from 5 males and 4 females and 3 pupal pelts and 4 larval pelts bred from tree holes.

The types will be deposited in the British Museum (Natural History).

Key to Ethiopian Species of *Megarhinus*.

1. Lateral tufts of 7th abdominal tergite black 2.
These tufts orange, golden, or red 6.
2. Lateral tufts of 8th tergite orange 3.
Lateral tufts of 8th tergite black *evansae* Edwards.
3. Lateral tufts of 6th tergite mainly white; black hairs, if present, very few at apex of segment 4.
Lateral hairs of 6th tergite largely black 5.
4. Female: second segment of mid tarsi with a broad white ring basally; third all dark. Male: hind tarsi without long hairs at the base of 1st segment; penultimate segment of palpi with a few very short bristles on inner and outer surfaces, those on outer surface the same length as those on inner surface *brevipalpis* Theobald.

- Female: segments 2-3 of mid tarsi all white. Male: hind tarsi with long hairs at base of first segment; penultimate segment of palpi with a number of hairs on inner and outer surfaces, those on outer surface conspicuously longer than, one or more at least twice as long as, the hairs on inner surface *barbipes* Edwards.
5. Female: second segment of mid tarsi with a broad white basal ring; third all dark. Male: hind tarsi without long hairs at the base of first segment; 5th sternite with a large triangular patch of white scales, which may or may not be interrupted in the middle subsp. *conradti* Grunberg.
- Female: segments 2-3 of mid tarsi all white. Male: hind tarsi with long hairs at the base of first segment; 5th sternite nearly all white *phytophagus* Theobald.
6. Lateral tufts of tergites 6-8 orange or golden 7.
These tufts red 8.
7. Abdominal tergites coppery golden colour; sternites bright golden yellow with no dark markings, except perhaps on seventh segment *lutescens* Theobald.
- Abdominal tergites bright purple; sternites bright golden yellow with a median line of dark purple scales on each segment *nairobiensis* sp. n.
8. Sternites with a median longitudinal stripe of dark purple scales on segments 2-6 *kaimosi* sp. n.
- Sternites 2-6 all golden 9.
9. Red caudal tufts large; male palpi with penultimate segment bristly above and hairy beneath; abdomen purple *erythrurus* Edwards.
- Red caudal tufts smaller; male palpi with few bristles and no hairs 10.
10. Tergites 1-3 green scaled; mid coxae with white scales at base *viridibasis* Edwards.
- At most tergite 1 green; mid coxal scales all golden *aeneus* Evans.

ACKNOWLEDGEMENTS.

I wish to thank Dr. Garnham, Mr. Harper, and Mr. Highton for allowing me to examine their series of *Megarhinus* from the Kaimosi Forest, and Dr. V. G. L. van Someren and Mr. Teesdale for lending me specimens of *M. brevipalpis*, and my husband Mr. G. R. Cunningham van Someren for the figure of *M. nairobiensis*.

REFERENCES.

- EDWARDS, F. W., 1941, *Mosquitoes of the Ethiopian Region*. Part III.
HOPKINS, G. H. E., 1936, *Mosquitoes of the Ethiopian Region*. Part I.
MACFIE, J. W. S., and INGRAM, A., 1922, *Bull. ent. Res.* 13: 410.
THEOBALD, F. W., 1910, *Monograph of the Culicidae* 5: 102.

Vol. 97. Part 8. Pp. 187-212, 15 figs.

21st October, 1946.

THE

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

X HICKIN, N. E., Ph.D., F.R.E.S. Larvae of the British Trichoptera	187-212, 15 figs.
---	-------------------

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

LARVAE OF THE BRITISH TRICHOPTERA

By N. E. HICKIN, Ph.D., F.R.E.S.

Manuscript received 25th September, 1945.

(Read 5th June, 1946.)

WITH FIFTEEN TEXT-FIGURES.

INTRODUCTION.

THE series of papers appearing in the *Proceedings of the Royal Entomological Society of London* (Series A) under the title of "Larvae of the British Trichoptera" is the outcome of some work commenced in 1937. The object was to describe the larvae of this not inconsiderable group from actual British specimens, and thus evolve reliable keys for identification based solely on British collections. Considerable stress was to be laid on figures as it was recognised that a large number of workers on general ecology and faunistic work concerned with fresh-water biological problems and fisheries, as well as specialists in the Trichoptera, would require to determine specimens without the laborious trouble of rearing them through to the adult stage. Already, some of this work has been hampered by the lack of suitable keys and descriptions. The author hopes that the present series of papers will remedy this and provide a suitable foundation for subsequent biological work. The task is rather a heavy one as Mosely in 1939 described the adults of as many as 185 species. In 1942 Kimmins added *Cyrrnus insolutus* McLachlan to the list and Canon Grensted and his sons have also added *Ithytrichia clavata* Morton and *Hydropsyche saxonica* McLachlan, thus increasing it to 188, and it is certain that further species will be added as this Order becomes more widely collected.

As the description of such a large number of larvae—many of which are rare or extremely local—is probably the work of a lifetime, it was thought desirable to publish the work in small separate papers as each species was studied. When the descriptions of a natural group of larvae have been completed then a key for determination will be included. This method has some disadvantages, but also does show some advantages. It will be seen that a few errors of hasty inference or faulty technique in the earlier papers have been corrected in some of the later work. A collection of pupae and pupal skins is also being made so that it is hoped sometime in the future to describe the pupae of the British Trichoptera and to evolve suitable keys for their determination.

Acknowledgment.

The author owes a heavy debt of gratitude to Mr. Martin E. Mosely of the Department of Entomology, British Museum, without whose generous help and encouragement over a long period this work would not have been accomplished. Mr. Mosely has confirmed the determination of all the reared adults and he has also examined and determined several collections of adults made in different localities.

To Mr. N. D. Riley, Keeper of the Department of Entomology, British Museum, also, the author is deeply indebted for the initial introduction to the subject and for the keen interest which he has displayed and for help in setting

out the text. Dr. E. B. Worthington, the Director of the Freshwater Biological Association, is thanked for the keen interest shown in this work and especially for the help given when I have managed to spend short collecting holidays at the Wray Castle Laboratories of the Association. To Dr. F. I. van Emden I am indebted for help in the description of the morphology of the caddis larvae. Lastly to my wife, my companion in field work, who has suffered the innumerable and ever-present dishes of stagnant water about the household *almost* without comment.

Method.

After many failures to maintain alive broods of caddis larvae hatched from egg masses (especially difficult through the winter months) it was decided to collect half-grown to fully-grown larvae from lakes, ponds, rivers, and streams where there was little or no possibility of mixing closely allied species. When possible, examples of the same species from different parts of the country were compared before the figures and description were made. When collected, half the examples were killed and preserved in "collecting fluid" recommended by Mosely, viz. two parts of 2% formalin to one part of 90% alcohol. This fluid thoroughly penetrates the specimens, which, as soon as convenient, were transferred to 2% formalin as this does not discolour as badly as the mixture with alcohol; but even so the thick white abdomens of many Limnophilid larvae will probably blacken.

The remainder of the specimens collected were then reared to maturity in flat enamelled dishes or small aquaria. In the dishes and aquaria a few alga-covered stones, some easily grown waterweed such as *Callitriche* and a root of a marginal plant such as *Veronica becca-bunga* were placed.

The latter was useful for many species, as providing a stepping-out place for the pupa for the final metamorphosis. Over each dish or aquarium a cotton gauze cloth was secured, usually with rubber bands, so as to confine the adults. The waterweed was changed from time to time as much of it was eaten by herbivorous and omnivorous types, sometimes leaving only the larger stalks. In the case of carnivorous larvae the changing of the weed introduced a new batch of small insects and crustacea to be trapped and devoured.

Up to the present time twenty-four species have been reared from larva to adult, representative of nine of the thirteen families. The task has been accomplished without artificial oxygenation of the water but this will almost certainly be necessary for rearing some species: other practical difficulties will be attendant such as the maintenance of an even, cold temperature in small aquaria in summer months. It may be necessary to use metal gauze breeding-cages permanently fixed in the natural habitat.

Collecting methods necessarily varied with the type of habitat. In deep weedy pools a strong pond net was employed or a grapnel fixed to a strong line. By this latter means weed was brought to the shore and inspected frond by frond. In the case of pool margins and slow shallow streams collections can be made by hand-picking. This necessitates the wearing of waders and working in a fairly strong light. Mention should be made of an aid to collecting in rippled water when collecting by sight. This is illustrated and described by Darling in his book *Island Home* and consists of a water-tight box with no lid and with the bottom made of glass. This is held in the water, nullifying the effect of the disturbed surface, so that the bottom can be seen quite plainly.

In streams and rocky lake-shores, stones should be turned over carefully as they often conceal groups of the larvae; indeed one sometimes suspects a

gregarious habit, *Stenophylax Kolenati* species behaving in this way. Submerged tree-trunks are worthy of close inspection as larvae often conceal themselves in the bark.

A large number of species travel quite well in collecting bottles at least for a few hours, if packed in wet weeds. But it is lethal to keep them in small containers half full of water so that they are shaken about in a haversack with the gradual increase of the temperature of the water. On the other hand, some species will live for a remarkable length of time out of water. For example, Mr. Mosely reports that he has found larvae of *Brachycentrus subnubilus* Curtis alive in an empty bait-can several weeks after it had contained water. In addition the author has often found that larvae (*Leptocerus alerrimus* Stephens and *Stenophylax stellatus* Curtis) will crawl half out of water lacking oxygen and remain so for several weeks.

As many features as possible were described from living larvae. Much can be learnt from a close observation of the habits of the living animal, even of its morphology. Most of the morphological features were made out from freshly-killed material in dilute glycerine with $\frac{2}{3}$ -inch and $\frac{1}{6}$ -inch objectives. Permanent mounts were afterwards made in balsam. It was, however, sometimes necessary to soften some of the more heavily sclerotised parts by boiling with 10% caustic potash solution in order to see obscured detail. This was often the case with larvae collected from stagnant pools when the front of the head was dirty with mud particles caught in the minute spicules (a feature of some LIMNOPHILIDAE) and sometimes carrying a considerable flora. In these cases treatment with caustic potash was necessary to clear away the detritus.

All the figures have been drawn by the author, unless stated otherwise in the text, from British material.

Literature.

Considering the pre-eminent work of McLachlan, and the very important contributions of Morton and Mosely to our knowledge of the adult British caddis flies, it is remarkable how little has been published on their larvae by British authors. However, there are several papers by Morton, and in Mosely's *Dry Fly Fisherman's Entomology*, and his *Insect Life and the Management of a Trout Fishery*, there are illustrations of some larvae and their cases. In addition, there is a chapter devoted to the life history of the caddis in Miall's *Natural History of Aquatic Insects*, which, although mainly quotation and treated in a somewhat elementary manner, yet remains to-day widely read by students of freshwater biology. Because of this lack of British information, workers on faunistic problems have been compelled to use the keys given in the numerous foreign publications on the trichopterous larvae, and consequently, when results have not been checked with the British list of adults, many determinations have been necessarily incomplete if not erroneous.

Perhaps Ulmer's work has had the most profound effect on the study of the life history of Trichoptera. The amount of study accomplished by this author in what was almost a virgin field is remarkable. His most important contributions to the knowledge of the larvae were published in a series of papers entitled "Beiträge zur Metamorphose der deutschen Trichopteren" in the *Allgemeine Zeitschrift für Entomologie* and subsequently collected together in parts five and six of Brauer's *Süsswasserfauna Deutschlands* published in 1909. The larvae of the Finnish species were described by Siltala in a series of papers from 1902 to 1908 in *Acta Societatis pro Fauna et Flora fennica*. (It should be borne in mind that in 1906 this author changed his name from Silfvenius to

Siltala, an earlier form of the same name.) Second only to Ulmer's work in importance is that of Lestage, to be found in Rousseau's *Larves et Nymphes Aquatiques des Insectes d'Europe* published in 1921. This work, together with that of Ulmer, is widely consulted by workers in this country. Other European workers who have made important contributions to the knowledge of trichopterous larvae are Reaumur (1737), Struck, Wesenberg-Lund, Thienemann, Martynov, Klapálek and Esben-Petersen.

In America, the larvae of many of the American species are considered in the *New York State Museum Bulletin No. 292* by Betten, published in 1934. This includes three special chapters by Kjellgren, Orcutt and Davis on larvae and their habits and refers also to the work of Krafka. An excellent bibliography on Trichoptera, which must be almost complete, is also included.

The nomenclature in the present papers for the British species is that used by Mosely in 1939 in *The British Caddis Flies*.

GENERAL MORPHOLOGY.

The Trichoptera are endopterygous insects placed by Tillyard in the Panorpid complex. Schwanwitsch, in his recent tabular classification, has placed the Order horizontally in the Inferiores position. On the more primitive side they are related to the PANORPIDAE in the Mecoptera, whilst on the more highly developed side they are related to the MICROPTERYGIDAE in the homoneurous Lepidoptera. They were included formerly in the Neuroptera but have been recognised as a separate and distinct Order for many years.

Trichoptera have truly aquatic branchio-apneustic or apneustic larvae, the whole larval state being spent in some aquatic habitat. The type of habitat ranges from torrential stream to stagnant ditch. A species found in fast-running streams is usually confined to this type of water, whilst those found in lakes and ponds are usually similarly restricted. Some species, however, have a rather wider range of habitat. Thus larvae of *Phryganea grandis* L. and *Mystacides nigra* L. are found on fairly open lake shores, weedy pools and also rivers. Oxygen for respiration is absorbed from the water, either by means of gills of various types or directly through the cuticle. *Enoicyla pusilla* Burmeister lives in damp moss at the roots of trees, but so far no detailed study of the morphology of the larva of this species is available, so that whether aquatic or terrestrial characters are shown must be temporarily left in doubt.

Three distinct types of trichopterous larva are fairly readily discernible. The eruciform larva (fig. 1) is typical of the families LIMNOPHILIDAE, LEPTOCERIDAE, SERICOSTOMATIDAE, MOLANNIDAE and ODONTOCERIDAE. The cylindrical abdomen, which is most often whitish but sometimes light green in colour, is protected by a case made of various materials such as sand particles or vegetable debris cemented together, and when alarmed the larva withdraws completely into it. The head is hypognathous and the first abdominal segment is furnished with three protuberances, one being median dorsal and the remaining two lateral. The shape of the case or the type of material used is characteristic of many genera and in some particular cases even of species.

The suberuciform larvae (fig. 2) of the PHRYGANEIDAE are in some respects similar to the eruciform larvae; thus they bear cases, but on the other hand the intersegmental grooves in the abdomen are deep, whilst in the eruciform larvae the grooves are shallow. In addition the head of the suberuciform larva is not hypognathous but is somewhat between this type and the prognathous type. Frequently the abdomen is coloured, and a colour pattern is present. In fact,

the suberuciform type of larva is intermediate between the eruciform larva and the campodeiform type which follows.

The campodeiform larva (figs. 3 and 4) differs widely from the eruciform and suberuciform types. Usually no case is constructed and the larva spins a net attached to the underside of stones or to the stems of plants. Small insects and crustaceans are caught in the web and are devoured by the larva. The net-spinning type of larva constructs a case immediately prior to pupation. The head is prognathous, which distinguishes it from the eruciform and suberuciform types. In habit the campodeiform larvae are more agile than are the eruciform

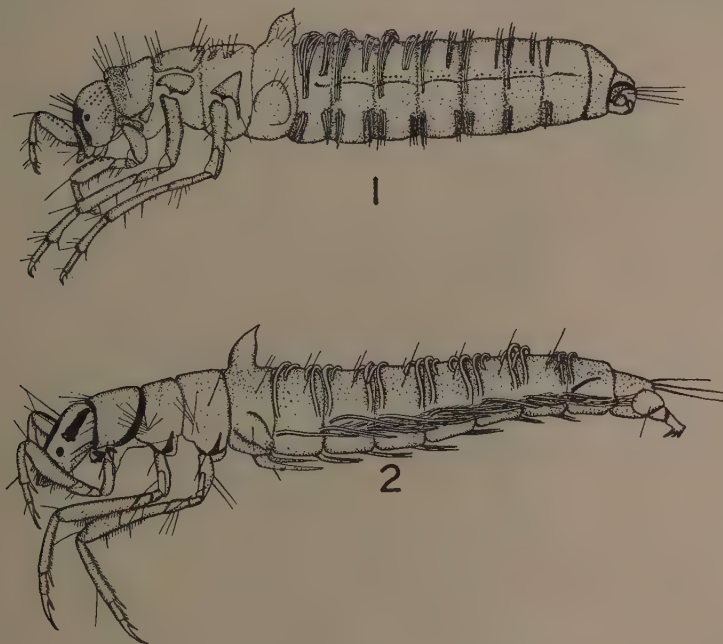


FIG. 1.—Eruciform larva of *Limnophilus* sp.

FIG. 2.—Suberuciform larva of *Phryganea* sp.

larvae and, as is to be expected, many of the characters associated with case-bearing are absent or modified. The anal claspers called by Orcutt the anal "prolegs," in the case-bearing types are short and thick, whilst in net-spinning and free types they are long and slender. In the former, the claws of the anal claspers enable them to retain their position inside the cylindrical case, whilst in the latter the claws are for holding position on the threads of the web, much as do those of the spider. The uniformly cylindrical abdomen of the eruciform larva is often replaced in the campodeiform form by a dorsoventral flattening and an anterior and posterior diminution in the size of the segments, the third or fourth segment of the abdomen often being the largest. Campodeiform larvae (the "thysanuriform" larvae of Orcutt) are characteristic of the families, RHYACOPHILIDAE, HYDROPTILIDAE, PHILOPOTAMIDAE, HYDROPSYCHIDAE, POLYCENTROPIDAE and PSYCHOMYIDAE.

Cuticular formations.

The cuticular formations of trichopterous larvae require some elucidation in order that the terms may bear some homology with the terms of previous authors. Siltala made a study of the chaetotaxy of the larva both in relation to the disproportionate spacing of the bristles, spines, hairs, etc., during larval growth, and also as regards variation in the different families. Orcutt gives some figures of the various cuticular outgrowths with a reference to Siltala's terminology in the text-figure legend.

In this morphological paper no account is given of the patterns of the larval case or of the traps or nets or other devices fabricated by the larva. It is hoped to include an account of these in another paper. Reference to

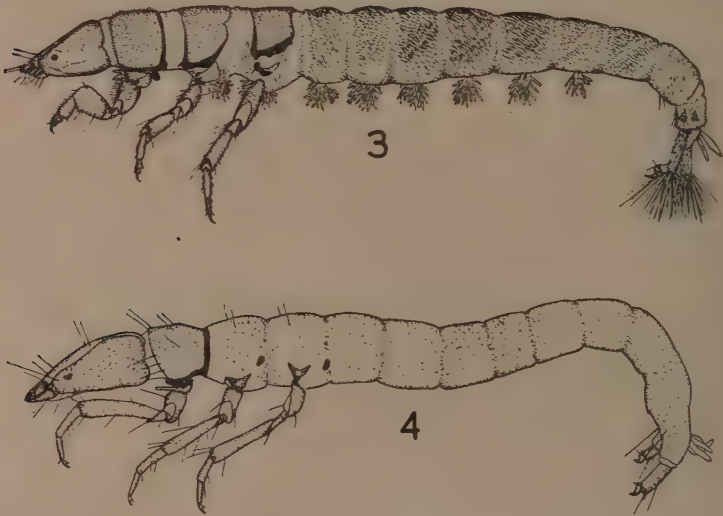


FIG. 3.—Campodeiform larva of *Hydropsyche* sp.

FIG. 4.—Campodeiform larva of *Philopotamus montanus*.

them, however, with figures, has generally been made by the author in his descriptions of individual larvae (see Bibliography).

Arising from the head, legs and anal segments of the larva are long stout bristles almost always dark in colour and with a light coloured ring at the base which is probably a local thinning of the membrane, allowing the bristle to articulate. These bristles are typical sensillae and are the "Borsten" of Siltala. The golden-yellow, thick, sword-shaped spines which are a characteristic feature of the ventral edge of the femur and tibia of many larvae are the "Sporne" of Siltala. Sometimes the spines are hairy (Federsporne) as in the tarsus of *Holocentropus* McLachlan and other POLYCENTROPIDAE. Sometimes a series of very small spines are situated along the ventral edge of some of the leg segments—these are Siltala's "Spörnchen." Other outgrowths and modifications of the bristles, spines and claws are dealt with later in the text.

The Head.—The head is a hard sclerotised capsule roughly in the shape of a truncated cone with the base hemispherical, the latter being the proximal part of the head at its insertion into the membranes of the prothorax. Variation in

the shape of the head amongst the different families is shown in fig. 5. In *Rhyacophila* Pictet the head is much longer than broad, whereas in *Molanna* Curtis the head capsule is equally as long as broad. In some cases, e.g. *Neuronia* Leach, the sides of the head (genae) are parallel, in others, e.g. *Silo* Curtis, the genae converge towards the mouthparts. The head capsule is made up of four distinct sclerites, firstly a three-sided sclerite, the clypeus, situated on the dorsal or anterior surface of the head with the vertex directed aborally and the base forming the anterior margin of the head capsule at the insertion of the mouthparts. There is some discussion, however, as to the true homology of this sclerite. Whereas Ulmer and Lestage together with most of the older authors have called this sclerite the clypeus, Orcutt prefers to call it the frons. According to Snodgrass, the frons has the muscles of the labrum attached, but I have not as yet been able to make out this musculature. The term clypeus is used for this sclerite throughout these papers.

In shape, the clypeus (fig. 6) is very roughly triangular with the lateral margins incised to a greater or lesser degree and often with the anterior lateral angles either extending or contracting. The clypeus of American species of *Chimarra* Leach is said to be asymmetrical. Bounding the clypeus are two large curved epicranial sclerites with a dorsal and a ventral suture. The dorsal suture extends from the vertex of the clypeus to the occipital foramen. The ventral suture extends from the submentum to the occipital foramen, but the two sclerites may be separated to a greater or lesser extent by the fourth sclerite known variously in the literature as hypostome, gula and gular sclerite. I have preferred to use the last term. The gular sclerite has many modifications, its shape being of taxonomic importance. In fig. 7 the range of shape of the gular sclerite is shown but although examples are given of the form in several families, the figures are not meant to imply that the shape shown is strictly typical for that family, but merely that it does occur in that family.

It has been pointed out by Siltala (1907) that the gular sclerite is not strictly homologous throughout the Order. Siltala considered that this sclerite in the case of the HYDROPSYCHIDAE was the mentum. If the whole range is compared it is quite apparent that the hard corneous or sclerotised anterior margin of the gular sclerite seen in the PHRYGANEIDAE, LIMNOPHILIDAE, SERICOSTOMATIDAE and ODONTOCERIDAE may be part of the true submentum. Indeed, in the SERICOSTOMATIDAE on the one hand and RHYACOPHILIDAE on the other, we see intermediate steps in the suppression of the gular sclerite and the elaboration of this corneous region forming the basal or aboral sclerite of the submentum. These modifications are, of course, closely associated with the feeding habit of the larva. The elongated prognathous head of HYDROPSYCHIDAE, PHILOPOTAMIDAE and RHYACOPHILIDAE, carnivorous, non-casemaking types, all show an extensive gular suture where the gena of each side meets in the mid-ventral line. The POLYCENTROPIDAE also show this, although the head is more globular: I suspect the latter feature as being secondarily produced. In the PHRYGANEIDAE and some SERICOSTOMATIDAE the epicranial margins are thickened and folded.

The attachment of the head muscles to the head sclerites is quite often distinctive, and is often the cause of characteristic if somewhat variable designs of small elliptical light-centred marks. The dark pigmented bands and designs are sometimes associated with these "muscle spots" and often, e.g. *Neuronia* Leach, *Phryganea* L. and *Mystacides* Latreille, the deep pigmentation on the yellow sclerites gives to the head of the larva a striking and handsome appearance.

Minute sclerotised spicules are sometimes a feature of the head sclerites.

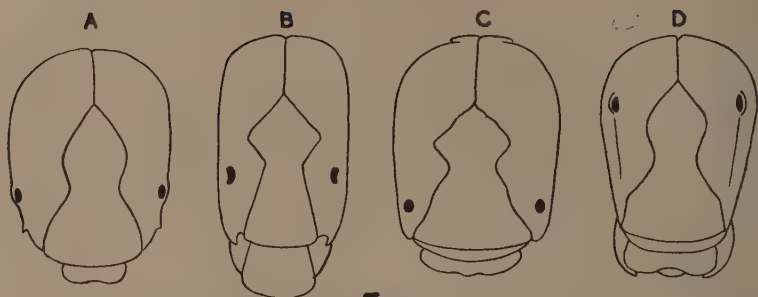


FIG. 5.—Types of larval head: A. *Limnophilus flavicornis*; B. *Rhyacophila dorsalis*; C. *Polycentropus flavomaculatus*; D. *Goëra pilosa*.

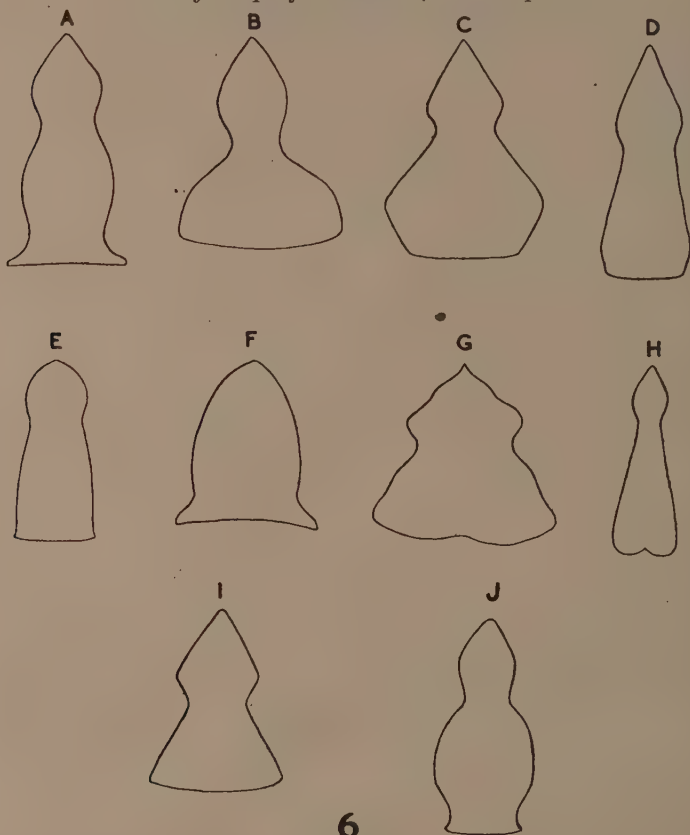
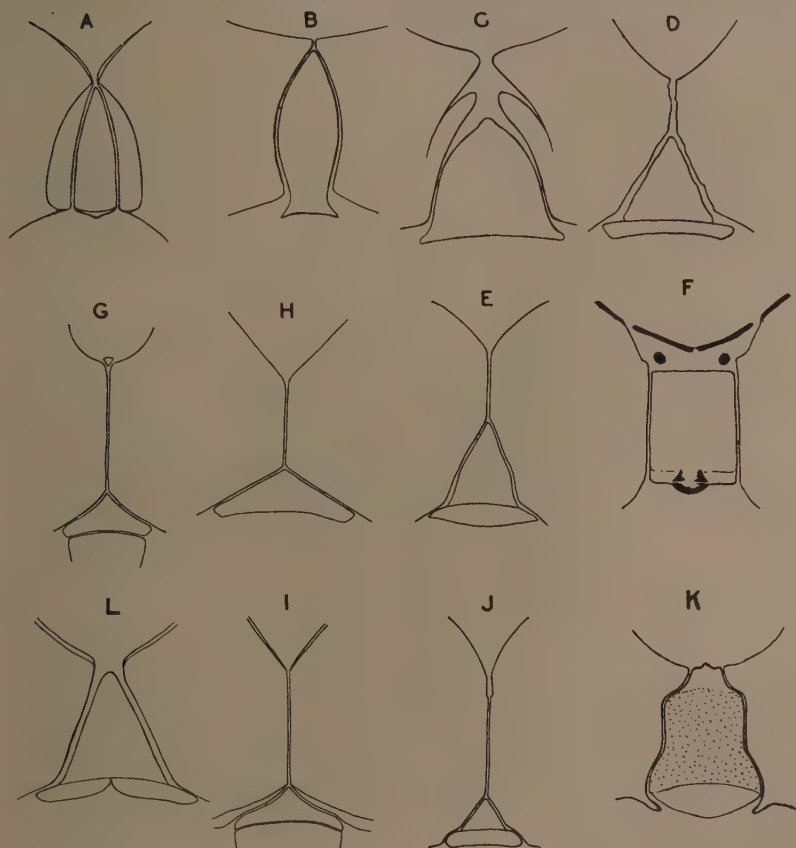


FIG. 6.—Types of larval clypeus: A. PHRYGANEIDAE (*Neuronia ruficrus*); B. LIMNOPHILIDAE (*Limnophilus flavicornis*); C. SERICOSTOMATIDAE (*Silo pallipes*); D. ODONTOCERIDAE (*Odontocerum albicorne*); E. LEPTOCERIDAE (*Setodes argentipunctella*); F. HYDROPSYCHIDAE (*Hydropsyche* sp.); G. POLYCENTROPIDAE sp.; H. PHILOPOTAMIDAE (*Philopotamus montanus*); I. RHYACOPHILIDAE (*Rhyacophila dorsalis*); J. SERICOSTOMATIDAE (*Lepidostoma hirtum*).

In the LIMNOPHILIDAE it is apparently confined to the head and a few other sclerites, but in the HYDROPSYCHIDAE the spicular condition is general throughout the body. In a few cases (*Lepidostoma hirtum* Fabricius, for instance) the head sclerites are finely sculptured. The chaetotaxy of the head of the tricho-



7

FIG. 7.—Types of larval gular sclerite: A. PHRYGANEIDAE (*Neuronia ruficrus*); B. LIMNOPHILIDAE (*Anabolia nervosa*); C. SERICOSTOMATIDAE (*Lepidostoma hirtum*); D. SERICOSTOMATIDAE (*Goëra pilosa*); E. ODONTOCERIDAE (*Odontocerum albicorne*); F. LEPTOCERIDAE (*Mystacides nigra*); G. HYDROPSYCHIDAE (*Hydropsyche* sp.); H. POLYCENTROPIDAE (*Holocentropus dubius*); I. PHILOPOTAMIDAE (*Philopotamus montanus*); J. RHYACOPHILIDAE (*Rhyacophila dorsalis*); K. MOLANNIDAE (*Molanna angustata*).

pteroous larva has been worked out by Ulmer. According to this author, the clypeus typically bears thirteen bristles, of which seven are situated on the anterior margin, one of these being in the middle and three associated with each lateral angle; of the remainder, three are situated near each lateral margin, one being aborally placed and two orally. There is often a diminution in this

number, sometimes the median bristle of the anterior margin being lost. Often, however, the number is increased, usually by an addition to the bristles in the lateral angles.

The eyes of all trichopterous larvae are small and it would not appear that visual sight plays an important part in their natural economy. Observation of larvae in aquaria gives this impression; thus in the chapter "Habits of the Trichoptera" by M. B. Davis in Betten's *Report on the Trichoptera of New York State*, she states that *Hydropsyche* Pictet larvae were unconscious of the presence of their prey until it actually touched them. Whilst this is being written a small number of *Phryganea grandis* L. larvae are in front of me in an aquarium. The method of progression when feeding is to make jerky forward strokes with both prothoracic legs, dragging the case behind. If anything is caught up by the sickle-like legs, it is immediately brought up to the tip of the mouthparts and apparently "felt," "smelt" or "tasted." If it happens to be a piece of vegetable debris it is rejected, but if a soft-bodied insect is caught it is devoured whilst held by the locked prothoracic legs. It is probable that sight is required only for distinguishing between light and dark—the habit of many larvae (e.g. *Stenophyllax Kolenati*) of hiding under stones during the daytime is well known.

The eyes appear as small patches of black pigment situated on the genae, sometimes in small convexities with the sclerotisation somewhat hyaline. Pigmentation of the chitin is usually absent from the area adjacent to the eye. This area sometimes appears as an oval white patch as in some of the POLYCENTROPIDAE. On the other hand, the eyes of *Silo pallipes* Fabricius are more deeply set into the head. Wesenberg-Lund has pointed out the relation between the feeding habits and the position of the eyes. Carnivorous larvae have eyes situated close to the anterior margin of the genae whilst in herbivorous types they are set much farther back. Omnivorous larvae have the eyes intermediate in position.

Excepting in the LEPTOCERIDAE, the antennae are never conspicuous. In many cases, antennae, in the fully grown larvae, are atrophied; they are always present, however, in the young larvae but degenerate at a later stage. In the LEPTOCERIDAE the antenna consists of a proximal bulbous and a long, filiform, distal segment furnished with a sensory bristle. In several other families the distal segment is short but there are usually some sensory bristles or rods which may be quite long as in *Agraylea* Curtis and *Oxyethira* Eaton or finger-like as in *Agapetus* Curtis.

The fairly typical mandibulate "biting" mouthparts show a range of form, which, if not very diverse, is at least quite important for determination of genera. A large membranous anteclypeus partially folds over the labrum. The anteclypeus is normally colourless, transparent and devoid of marking but in the POLYCENTROPIDAE it is divided into four dark areas by three longitudinal white lines. The labrum (fig. 11, A, B, C, and D) is almost always yellowish, transversely elliptical with an incision in the middle of the anterior margin. The incision varies in extent and is absent in *Rhyacophila* and *Hydropsyche*. However, in the PHILOPOTAMIDAE are seen some remarkable deviations from the typical labrum. In *Philopotamus* Leach it is elongated longitudinally and has the anterior lateral areas extended into prongs.

In *Chimarra* the labrum is intermediate between this extreme and the typical form. Some black bristles and yellow spines are variously placed on the labrum, often one or two pairs of curved spines are situated on the anterior margin directed towards the median incision. In some species a cushion-like protuberance covered with minute spines is situated immediately posterior to

the incision and probably has a sensory function. The ventral surface of the labrum has hairy tracts, and further spines are generally present.

The mandibles (fig. 8) are heavily sclerotised and are deep chestnut brown to black in colour. They are roughly divisible into two main types, supposed by various authors to be correlated with the feeding habits of the larvae. In many cases the mandibles are markedly asymmetrical. In the PHILOPOTAMIDAE, POLYCENTROPIDAE and some of the RHYACOPHILIDAE the mandibles are sharply pointed at their outer tip with a cutting edge along the inner margin

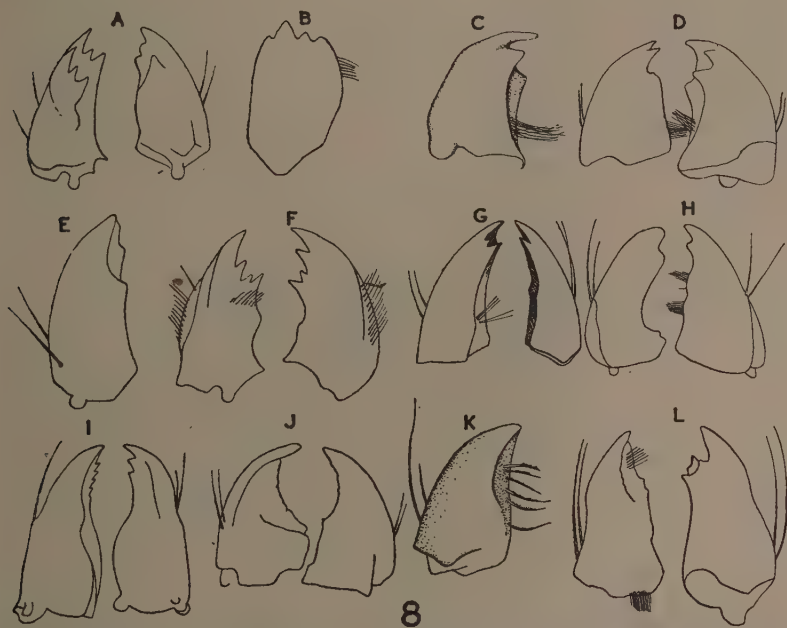


FIG. 8.—Types of larval mandible: A. PHRYGANEIDAE (*Phryganea striata*); B. LIMNOPHILIDAE (*Stenophylax stellatus*) (left); C. SERICOSTOMATIDAE (*Lepidostoma hirtum*); D. BERAEDAE (*Beraea maurus*); E. LEPTOCERIDAE (*Mystacides nigra*); F. HYDROPSYCHIDAE (*Hydropsyche pellucidula*); G. POLYCENTROPIDAE (*Cyrnus flavidus*); H. PSYCHOMYIDAE (*Psychomya pusilla*); I. PHILOPOTAMIDAE (*Wormaldia subnigra*) (from below); J. RHYACOPHILIDAE (*Rhyacophila dorsalis*); K. RHYACOPHILIDAE (*Agapetus fuscipes*); L. HYDROPTILIDAE (*Oxyethira costalis*).

Fig. 8, D, F, G, H, I and L after Lestage.

which may be knife-like as in *Philopotamus* or sickle-like as in *Rhyacophila*. The numerous well-defined teeth in the HYDROPSYCHIDAE and PHRYGANEIDAE are well adapted to gripping and tearing. In the LIMNOPHILIDAE the teeth are almost always blunt, and if present at all a cutting edge on the inner margin is little developed. Although I have observed the larvae of *Chaetopteryx villosa* Fabricius devouring *Veronica becca-bunga* plants piecemeal, yet limnophilid mandibles more often seem to scrape a layer of tissue off the plant organs. Two bristles occur on the outer edge of both mandibles in most species but the occurrence of a brush of smaller hairs or bristles on the inner edge is somewhat

variable. In some families the brush occurs on both mandibles (e.g. BERAEEIDAE) and such types are said by Siltala to be phytophagous and where they are absent (*Rhyacophila*, *Wormaldia* McLachlan, *Philopotamus*) the types are carnivorous (but not always entirely so). In the cases where the brush is present on one mandible and not on the other the larva may be phytophagous, carnivorous or omnivorous. In some types thick blunt hairs are found, and in *Agapetus fuscipes* Curtis there are a number of curious branched bristles on the inner edge.

The cardo of the maxilla on each side is attached to the submentum of the labrum at its base, and most figures in the literature show the maxillae and labium undivided. The maxilla (fig. 9) consists of cardo, stipes, maxillary lobe (the inner lobe) and the palp. Cardo and stipes are both broad structures, sometimes hairy, often bearing bristles, and sclerotised bands are often conspicuous. Great variation attends the shape of the maxillary lobe where one or, in some cases, both endites are suppressed. In some families—PHRYGANEIDAE, ODONTOCERIDAE, HYDROPSYCHIDAE, POLYCENTROPIDAE and RHYACOPHILIDAE—the lobe is long, almost as long as the maxillary palp, and finger-like with the tip furnished with sensory papillae and rods. In some cases, as in *Holocentropus* McLachlan, the lobe is furnished with some inwardly directed yellowish spines, but more often, as in *Neuronia* and *Odontocerum* Leach, the spines arise from the broadened proximal base of the maxilla. *Lepidostoma hirtum* and *Goëra pilosa* Fabricius both show flattened cushion-like lobes with the associated spines reduced to warty knobs. In *Tinodes waeneri* L. a similar cushion-like lobe is found but the spines are apparently suppressed. The maxillary palps are strong and sclerotised and consist usually of four segments inwardly curved. In the LEPTOCERIDAE there are often only three segments apparent, but in some other species of this family, the fourth (proximal) segment is just visible as a sclerotised patch on the outer side near the base of the maxillary lobe. Thus *Leptocerus aterrimus* Stephens and *Setodes argentipunctella* McLachlan both have four-segmented maxillary palps whilst *Triaenodes bicolor* Curtis has only three segmented palps. Some doubt exists amongst authors on the question of the number of segments. This has been mainly due to the occurrence in some groups of a horseshoe-shaped sclerite at the base of the palp which could or could not be considered as part of the palp. It appears that we are looking at an evolutionary change as yet only partly completed. I have not, as yet, collected material of *Oecetis* McLachlan, but from figures in the literature it appears that a similar process is carried even farther here so that only two complete segments are apparent.

A brush of hairs often arises from the base of the palp and sometimes these hairs are thick and blunt. The maxillae of *Philopotamus montanus* Donovan are strikingly different from the general type. They take the form of a pair of scoop-like sheaths edged with spines which close round, and seemingly protect the labium.

The labium is conical, sometimes hemispherical and sometimes with a beak-like projection (the ligula) at its distal end. The duct of the spinning organ opens at the tip of the ligula. Where the ligula is not prominent the spinning organ opens midway between the labial palps. This distal region is probably the fused glossae and paraglossae. The labial palps are usually distinct, sometimes prominent as in *Neuronia ruficrus* Scopoli; in other species difficult to discern, but they are vestigial in at least some of the PSYCHOMYIDAE. The number of segments is generally two, a proximal bulbous and a distal finger-like segment furnished with sensory papillae at the tip. (Often the sensory papillae

are well developed and may be of two segments.) The basal, proximal part of the labial palp must be considered a segment and not merely a protuberance of the labium, as in a few instances it is evident that it is clearly separated by a separate sclerite (e.g. *Neuronia ruficrus*). PSYCHOMYIDAE have a charac-

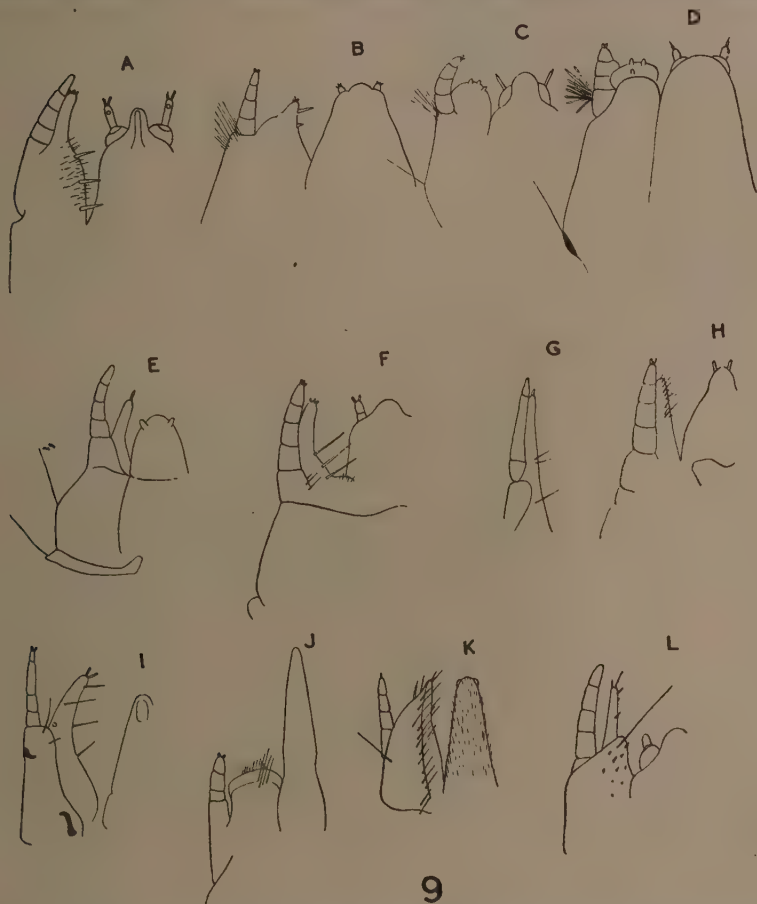


FIG. 9.—Types of larval maxilla and labium: A. PHRYGANEIDAE (*Neuronia ruficrus*); B. LIMNOPHILIDAE (*Limnophilus flavicornis*); C. SERICOSTOMATIDAE (*Lepidostoma hirtum*); D. SERICOSTOMATIDAE (*Goëra pilosa*); E. BERAIDAE (*Beraea maurus*); F. ODONTOCERIDAE (*Odontocerum albicorne*); G. LEPTOCERIDAE (*Oecetis ochracea*); H. HYDROPSYCHIDAE (*Hydropsyche pellucidula*); I. POLYCENTROPIDAE (*Holocentropus dubius*); J. PSYCHOMYIDAE (*Tinodes waeneri*); K. PHILOPOTAMIDAE (*Philopotamus montanus*); L. RHYACOPHILIDAE (*Rhyacophila dorsalis*).

teristic long acicular labium. Very often the curved bow-shaped internal sclerites of the mentum are clearly visible. The submentum is contiguous with the gula at its proximal extremity as mentioned previously.

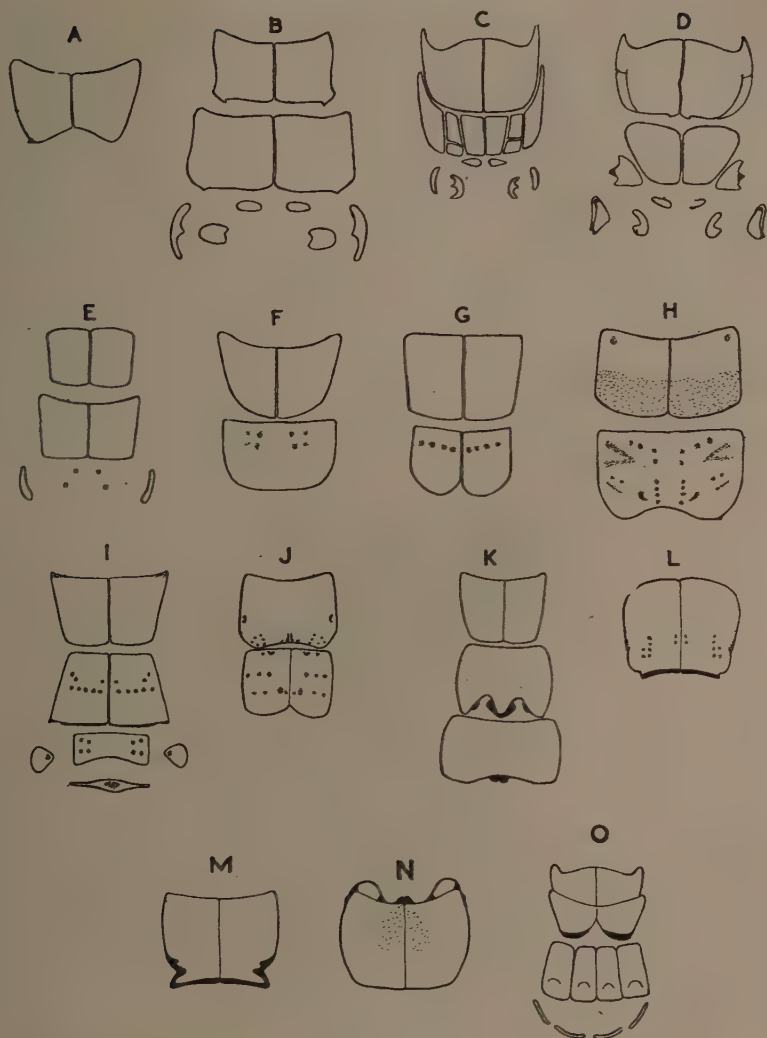
Thorax.—Larvae of Trichoptera are endopterygous, there being no external sign of developing wings. The three leg-bearing segments are quite distinct,

although in some instances the pronotum is closely associated with the aboral region of the head. This is the case in *Neuronia ruficus*, the head and pronotum forming one movable unit. In *Goëra pilosa* the head can be retracted into hood-like anterior extensions of the pronotum.

Sclerotisation of the thoracic nota (fig. 10) shows a considerable range of complexity throughout the Order. In the PHRYGANEIDAE, POLYCENTROPIDAE, *Rhyacophila* Pictet in the RHYACOPHILIDAE, and *Tinodes* Leach in the PSYCHOMYIDAE, only the pronotum is sclerotised. In the HYDROPTILIDAE and HYDROPSYCHIDAE all three thoracic nota are sclerotised. In some others such as the LIMNOPHILIDAE, ODONTOCERIDAE and the SERICOSTOMATIDAE the pro- and mesonotum are sclerotised with the metanotum largely membranous but with sclerotised patches furnished with bristles. The LEPTOCERIDAE are characterised by the pro- and mesonotum being sclerotised whilst the metanotum is entirely membranous. Finally, in some cases such as *Agapetus* Curtis in the RHYACOPHILIDAE, the pronotum is entirely sclerotised whilst the meso- and metanotum are only partially sclerotised. In many case-bearing larvae there is a membranous finger-like appendage which is known as the "prosternal horn." It lies between the prothoracic legs and is an outgrowth of the prosternum.

Legs.—The legs of trichopterous larvae are strongly developed, those of the eruciform types in most cases being more highly modified than those of campodeiform types. This is, however, contrary to what is expected by the use of the terms "eruciform" and "campodeiform." The leg is supported by an arched sclerite, the coxopleurite which is adherent to the pleural membrane, the trochantin bearing the condyles being variously modified. In *Triaenodes bicolor* Curtis, which swims largely by means of the fringed metathoracic legs, pulling its case behind, the trochantin is exceptionally long and black in colour. In all larvae the coxa is thick and strong with a deep incision on the dorsal surface of the distal margin of the sclerite which is covered with a thin membrane and allows the trochanter to move in an upward direction. The trochanter consists almost always of two divisions. In *Leptocerus aterrimus*, however, the trochanter of the metathoracic legs consists of three divisions but this is not general throughout the LEPTOCERIDAE, although there is a furrow in the metathoracic trochanter in some other species as though there were an incipient division. The divisions of the trochanter do not appear to exercise any separate movement and the proximal division is nearly always considerably smaller than the distal. Sometimes, as in the LEPTOCERIDAE, the trochanters are of considerable length. Very seldom does the proximal segment bear many bristles.

The femur is always the largest single sclerotised segment of the leg and often bears one or two black bristles dorsally, of considerable length, and also a series of spines on the ventral edge, which, in eruciform and suberuciform larvae, are often strong and of two distinct sizes, so that when the tibia and tarsus are pulled against the femur by the strong muscles which are present, the prey is very efficiently trapped. It is peculiar that this mechanism is not developed in the campodeiform types which are looked upon as typically carnivorous; the legs of the latter forms are quite innocent of such strong spines. The femur is inserted deeply into the distal segment of the trochanter, and previous authors have differed widely in making out the structures whereby these segments are attached. Siltala considers that the femora of meso- and metathoracic legs in the LEPTOCERINAE are divided into two segments. A. W. Orcutt adds to this and states that in *Mystacides* and possibly other LEPTOCERINAE



10

FIG. 10.—Patterns of sclerotisation of larval thoracic nota: A. PHRYGANEIDAE (*Phryganea grandis*); B. LIMNOPHILIDAE (*Limnophilus flavicornis*); C. SERICOSTOMATIDAE, GOERINAE (*Silo pallipes*); D. SERICOSTOMATIDAE, GOERINAE (*Goëra pilosa*); E. SERICOSTOMATIDAE, LEPIDOSTOMATINAE (*Lepidostoma hirtum*); F. SERICOSTOMATIDAE, SERICOSTOMATINAE (*Sericostoma personatum*); G. BERAÉIDAE (*Beraeodes minuta*) after Struck; H. MOLANNIDAE (*Molanna angustata*); I. ODONTOCERIDAE (*Odontocerum albicorne*); J. LEPTOCERIDAE (*Triaenodes bicolor*); K. HYDROPSYCHIDAE (*Hydropsyche* sp.); L. POLYCENTROPIDAE (*Holocentropus dubius*); M. PHILOPOTAMIDAE (*Philopotamus montanus*); N. RHYACOPHILIDAE (*Rhyacophila dorsalis*); O. SERICOSTOMATIDAE (*Brachycentrus subnubilus*).

the trochanters are divided into three segments. From the studies of *Leptocerus aterrimus*, *Triaenodes bicolor*, *Mystacides nigra* L., *Mystacides azurea* L. and *Setodes argentipunctella* my view is that in some cases the trochanters are divided in two and in others three. Where the division of the trochanter is into two parts the distal part may show a further division. The femur is always of one segment, but in this subfamily (LEPTOCERINAE) there is a considerable amount of articular movement between the femur and the distal segment of the trochanter. (In other groups the amount of movement is very limited.) Apparently there is a thin, light but strong membranous sheath forming a hinge between the segments; where this sheath joins the femur it gives the misleading appearance of a divided femur. Again, the ventral sclerotised wall of the distal segment of the trochanter extends upwards and inwards and forms an anvil against which the proximal end of the inserted femur can be levered by means of the muscles. It should be noted that in the LEPTOCERINAE the legs are very long and slender.

The tibia and tarsus each consists of a single sub-cylindrical sclerite, but in *Mystacides* both the tibia and tarsus show an incipient but not quite complete division in the metathoracic legs. In some campodeiform types the tarsus,

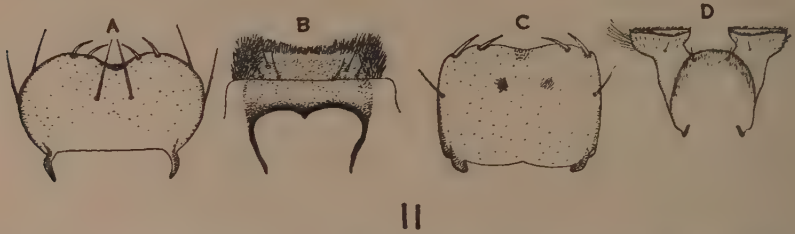


FIG. 11.—Types of larval labrum : A. *Neuronia ruficrus*; B. *Agapetus fuscipes*; C. *Setodes argentipunctella*; D. *Philopotamus montanus*.

and in addition sometimes the tibia, is covered with short hairs or spines which are said to serve as a brush for cleaning the nets. In connection with this observation, however, it should be mentioned that nets are found frequently which are completely silted up with fine mud. In *Holocentropus* there is a tuft of branched hairs at the distal extremity of the tarsal sclerite. The tarsus is terminated by a strong claw furnished with a spine at its base. (The spine in *Molanna* is longer than the claw.) The modifications of claw and spine offer useful characters for determination. The claw is perhaps least modified in some of the campodeiform types such as *Rhyacophila*.

Orcutt has called attention to the play of functional adaptation in the legs of trichopterous larvae. Thus in *Brachycentrus* Curtis, the femora of the prothoracic legs are short but very thick and strong. This is related to the habit of this species of anchoring the case to a frond of weed and seizing small insects and vegetable debris as they are carried past the opening of the case by the current. The long fringed metathoracic legs of *Triaenodes bicolor* with well-developed trochantin have already been alluded to in the text as serving for swimming. The short legs of most campodeiform net-spinning types such as *Phryganea* are other examples of this functional adaptation. Generally, in campodeiform types, the legs are approximately equal in size, whereas in cruci-form types the prothoracic legs are always shortest, usually held bunched up

under the head, whilst the metathoracic legs are longest but in some cases, e.g. some LIMNOPHILIDAE, the mesothoracic legs are slightly longer.

The author has figured the legs of twenty British species in his series of short papers, and the various points discussed above are readily seen in these figures, but in view of some errors of nomenclature which crept into some of the earlier papers (see *errata* at the end of this paper) the legs of *Limnophilus flavicornis* Fabricius have been re-figured (fig. 15, A, B and C).

Abdomen.—The abdomen is almost entirely membranous, very little sclerotisation being present on this part of the body. In eruciform larvae the abdomen is usually uniformly cylindrical or tapering to a small degree only. It is white or cream in colour but may be light green and with no colour pattern on the dorsal surface. There may be, however, a shield-shaped patch, sometimes sclerotised and furnished with bristles, and dark in colour on the dorsal surface of the ninth segment. The shape of abdomen of eruciform larvae is, of course, related to the case-bearing habit of this type of larvae. The abdomen is very seldom completely withdrawn from the case; in many species this may only happen if an accident occurs. In those species which cut off the tail end of the case when the head end is increased in size the anal claspers still retain a grip on the rim of the head end of the case. The intersegmental grooves in the abdomen of eruciform types are shallow, whereas in suberuciform and campodeiform types they are deep. In some campodeiform forms (POLYCENTROPIDAE) the abdomen is somewhat dorsiventrally compressed, but most are usually thickest at about the third segment; other campodeiform forms (PHILOPOTAMIDAE and HYDROPSYCHIDAE) have cylindrical abdomens. In HYDROPTILIDAE the abdomen is very distended at the fourth and fifth segments and is so reminiscent of some coleopterous eruciform larvae that it may be mistaken for a larva of this form. Campodeiform and suberuciform larvae are not usually white (*Philopotamus* is an exception). They may be green (*Rhyacophila* and *Hydroptila*), reddish-brown (POLYCENTROPIDAE), or greyish-brown (*Hydropsyche* Pictet), and a colour pattern may be present on the dorsal surface (*Neuronia*).

Most eruciform and suberuciform larvae bear three protuberances or "tubercles" on the first abdominal segment. One is disposed dorsally in the middle of the segment and the remaining two laterally. In species in which they are most developed (such as *Neuronia* and *Phryganea*) they are fleshy and finger-like and often bear sensory bristles or patches of small spicules (fig. 12, A). They are absent in free-living larvae, and often in eruciform larvae the median dorsal protuberance is absent. In some species, e.g. *Leptocerus aterrimus*, the lateral protuberances are not well developed, but the patches of sclerotised spicules are conspicuous and a spur-like black sclerite may be present (fig. 12, B and C).

Gills.—The aquatic habitat of the larvae has led to a closed tracheal system and to gill development. It is agreed with Orcutt that in many cases a large proportion of the oxygen absorption for respiration must be cuticular, yet gills of some type are almost always present. Several authors, such as Siltala and Orcutt, have made mention of localised patches of membrane on the coxa of each leg for oxygen absorption which occur in *Hydropsyche* and some POLYCENTROPIDAE, whilst in *Ithytrichia* Eaton the same function is undertaken by sac-like diverticulae on the pleural region of the third segment to the eighth segment. Amongst the more normal types of gill occurring in the Order there are simple filiform gills which may be covered with small black hairs (fig. 13, C) as in *Neuronia*, and may vary in length from a small conical process to a long

filament as long as, or even longer than, the abdominal segment from which it arises. On the other hand, many larvae bear compound gills (some species of *Rhyacophila* and *Hydropsyche*) which have the appearance of tufts of small gills arising from a common stalk or stalks (fig. 13, A). The number of gills present varies to a great extent throughout the Order, and indeed small variations are found within the species. Thus it is not wise to place undue reliance on the number of gill filaments in determining species, especially where closely related species are said to differ in respect of single gills. In general the gills

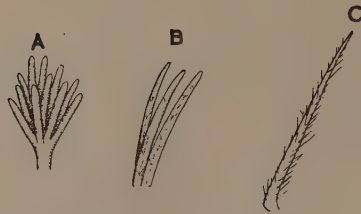
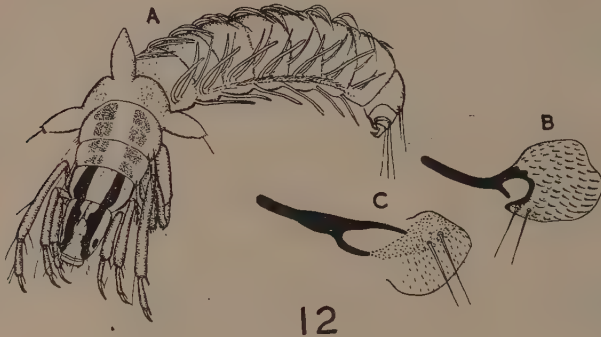


FIG. 12.—Abdominal protuberances: A. view of half-grown larva of *Neuronia ruficrus* showing protuberances; B. lateral sclerite on protuberance of *Mystacides nigra*; C. lateral sclerite on protuberance of *Leptocerus aterrimus*.

FIG. 13.—Types of gill: A. branched tracheal gill (HYDROPSYCHIDAE); B. blood gills (POLYCENTROPIDAE); C. simple tracheal gill (PHRYGANEIDAE).

occur as longitudinal series with dorsal, lateral and ventral rows. Transversely the gills occur at either the anterior or lateral, or both margins. The occurrence of gills in the different species is shown by Lestage (*in* Rousseau) in a tabular form. Gills are usually absent from the first abdominal segment but extend from the second to the eighth segment. Very seldom do tracheal gills occur on the ninth segment. All gills are directed posteriorly.

Blood gills (which are non-tracheated) occur in the Trichoptera only as evaginations of the anal region and are few in number, never exceeding six

(fig. 13, B). They are usually eversible: this is brought about by pressure exerted by the abdominal segments, and the retraction is carried out by an inserted branched muscle arising from the body wall. Many species have the habit of moving the abdomen in an undulating rhythmic manner in the vertical plane. This is most probably an accessory aid to respiration, causing a flow of water over the gills and the surface of the body. Campodeiform types such as some of the POLYCENTROPIDAE, suberuciform, for example, *Phryganea striata* L. and eruciform (*Limnophilus flavicornis*), all show this habit.

In all case-bearing larvae there occurs a tract of dark hairs running along the pleural region on both sides of the abdomen. This is known as the "lateral line." In its most highly developed condition it extends from the third abdominal segment to the eighth but is often lacking in some of the hinder or fore segments. Generally the lateral line is made up of two distinct lines of hairs and has been likened to a fold or wrinkle.

It should be mentioned, however, that some free-living larvae, such as some of the POLYCENTROPIDAE, show a hairy tract running along the pleural region of the abdomen. These hairs are long and not nearly so numerous as those in

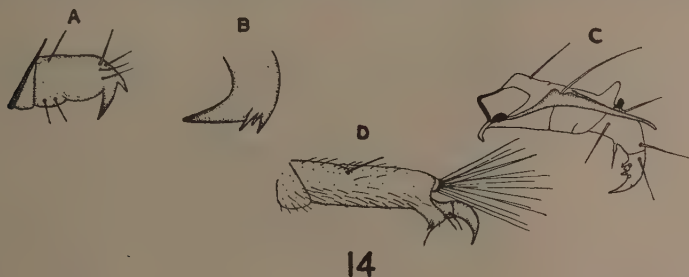


FIG. 14.—Types of anal clasper: A. claw of anal clasper of *Limnophilus lunatus*; B. tip of claw of clasper of *Mystacides nigra*; C. anal clasper of *Rhyacophila dorsalis*; D. anal clasper of *Hydropsyche* sp.

the lateral line of the case-bearing larvae. Probably associated with the "lateral line" is a series of very small sclerotised points or tubercles which are reddish-brown in colour. These occur in a small linear series just dorsal to the lateral line. There may be eight or less tubercles in each segment on each side in species where the tubercles are fully developed.

Anal Claspers.—All trichopterous larvae bear a pair of claws at the posterior end of the abdomen (fig. 14, A). These are situated on variously segmented appendages or pygopods which arise from the ninth abdominal segment. In case-bearing larvae these appendages are short and bulbous with the proximal segments much enlarged, often fused to form a tenth abdominal segment. With the free-living larvae the appendages are long and slender. These claws are very strong and when hooked into the silken lining of the case it is often impossible to remove the larvae without rupturing the abdomen. Even when the larvae is cutting away part of the hinder end of the case, it retains a grip on the silken lining of the case by means of the claws. In the free-living types the anal claws serve to grip the silken net when the larva is running backwards, which many of them do over their nets or down their silken tubes. The tips of the claws are directed anteriorly and often bear two or three smaller auxiliary hooks (fig. 14, B) and sometimes rows of small spicules. Much discussion has

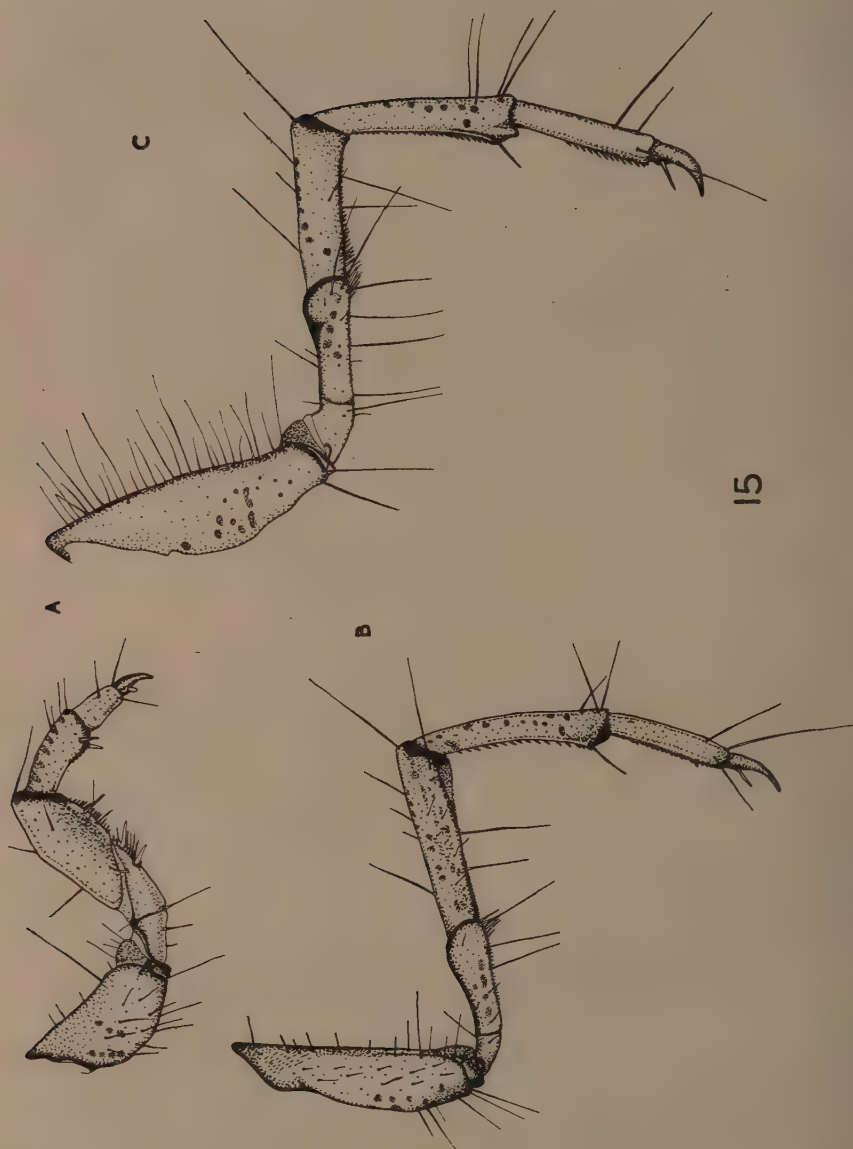


FIG. 15.—Legs of trichopterous larva (*Limnophilus flavicornis*): A. prothoracic; B. mesothoracic; C. metathoracic.

taken place on the homology of the segments of the claw-bearing appendages. Embryological studies have apparently not been carried out, but Siltala has put forward his views based on the positioning of bristles, and Orcutt (*in Betten*) has discussed them. Briefly, Siltala considers the typical trichopterous anal appendage (as found in certain POLYCENTROPIDAE) as being divided into four segments and as borne on the ninth abdominal segment. The first of the four segments is in two parts, the second is long and well sclerotised, the third is small, of soft interconnecting membrane, and dilated ventrally. The fourth segment, according to Siltala, is the highly sclerotised claw which is divided and bears bristles on both divisions. In general, the PSYCHOMYIDAE and PHILOPOTAMIDAE conform to this arrangement, but in the HYDROPSYCHIDAE there is some fusing of the proximal segments of the appendages as the larva develops, with a consequent shifting of the anal opening posteriorly. The very large number of bristles also somewhat confuses the normal interpretation of the segments (fig. 14, D). In the RHYACOPHILIDAE the arrangement of the bristles is again rather confusing, but in the HYDROPTILIDAE changes take place progressively during the larval life, but a tenth segment is formed during the later stages. In *Rhyacophila* a finger-like appendage arises from each pygopod (fig. 14, C). The tenth abdominal segment of the case-bearing larvae is composed of the first two segments of the anal pro-legs, and the two sclerites at the base of the claw (one usually being lunate), which are characteristic of these larvae, represent the other segments. In these larvae the anal opening is situated at the posterior line of fusion in the made-up tenth segment.

A KEY TO THE FAMILIES OF TRICHOPTEROUS LARVAE.

The difficulties in presenting a key to the families of trichopterous larvae are numerous. Firstly it will be seen that the classification of the Trichoptera, which has been almost entirely (except by Martynov) based on characters of the adult flies, certainly does not conform with the natural groups which I have found amongst the larvae. The SERICOSTOMATIDAE are one example of an assemblage rather than a natural group and *Agapetus* Curtis in the RHYACOPHILIDAE and *Enomus* McLachlan in the PSYCHOMYIDAE, as well as several others, occupy purely arbitrary positions. Ulmer, in his researches on the Trichoptera in Baltic Amber, pointed out in 1912 the polyphyletic nature of the SERICOSTOMATIDAE. Some authors, such as Martynov, have attempted to rectify this by alterations of the classification but inevitable complications have occurred, and as the object of this work is to present descriptions and keys which the general biological worker and freshwater biologist can use, the key has been kept as simple as possible within the well-known classification. As previously mentioned, the classification adopted by Mosely in his *British Caddis Flies*, a classification based upon the work of McLachlan and Ulmer, has been followed here. In addition, Mosely's book is the only one likely to be available referring only to the British species.

Although much help has been derived from the keys of Ulmer, Lestage (*in Rousseau*), and Krafka (*in Betten*), an entirely different approach has been made in the present key. It has been usual to make an initial splitting on the considerations of whether the larvae are of the campodeiform or eruciform types. To the general entomological student, the Trichoptera present some difficulties here. Not only do some species (PHRYGANEIDAE) exhibit both campodeiform and eruciform characteristics but several genera such as *Agapetus* are difficult to differentiate in this regard. Accordingly characters have been chosen which

are positive, such as the presence and shape of sclerotised areas on the thoracic nota, the clypeus and gular sclerite. Confirmatory differentiating evidence is also found in the nature of the case (in the case-bearing types) but such evidence must bear a purely secondary rôle, as a larva after collection often leaves its case and may invade the case of another. The present author has even found this in nature, having taken a half-grown specimen of *Phryganea striata* from the case of a fully grown example, and it is quite possible that different species may occupy each others' cases when driven out of their own.

The marking of the sclerites and the position of bristles have not been used as determining characters on account of variation of the former and the possible breakage of the latter. Larvae are often found on examination to have several bristles broken off close to the cuticle and only the circular pit is left.

It has not been possible at the present stage entirely to differentiate between larvae of the BERAETIDAE and those of the SERICOSTOMATINAE. Ulmer suggested that the BERAETINAE should be split off from the MOLANNINAE and placed with a nearer relationship to the SERICOSTOMATIDAE, and Mosely has described the genus *Beraeodina* which is intermediate between these two families. Thus the larval characters tend to confirm this view.

A Key to the Families of Trichopterous Larvae.

(Note: Figures and letters in brackets refer to the numbers of the text-figures to which reference is made as a guide in using the key. More detailed figures are given in the short separate papers, reference to which are given at the end of this paper.)

1. Metanotum entirely membranous 2.
- Metanotum sclerotised wholly or in part 10.
2. Mesonotum membranous 3.
- Mesonotum sclerotised 7.
3. Pronotum sclerotised with heavily sclerotised concave anterior margin, protuberant lobes on anterior margin absent (10, A). Larva is of suberuciform type. Large medium and two lateral lobes on first abdominal segment. Gular sclerite narrow longitudinally with adjacent areas of genae thickened into lobes and completely dividing genae (7, A). Larva bears a case made of vegetable fragments, cut leaves, stalks, etc., arranged spirally PHRYGANEIDAE.
- Pronotum sclerotised but not heavily sclerotised at anterior margin (3 and 4). Larvae of campodeiform type. Do not bear cases. Gular sclerite transverse and not dividing genae 4.
4. Labrum not sclerotised, elongated with transverse ciliated anterior margin (11, A). Clypeus extremely narrow (6, H) PHILOPOTAMIDAE.
- Labrum sclerotised and transverse 5.
5. Labium long, slender and pointed, projecting beyond the maxillary lobe (9, J). Gills absent except 5 anal gills. Lateral line absent PSYCHOMYIDAE except *Ecnomus*.
- Labium not projecting beyond the maxillary lobe 6.
6. Clypeus with sinuate margin and excised anterior margin (6, G). Abdomen brownish or reddish. Abdominal gills (except anal gills) absent. Gular sclerite simple (7, H) POLYCENTROPIDAE.
- Clypeus with single excision only on lateral margins (6, I). Anterior margin not excised. Abdomen green, sometimes with tufted gills. Gular sclerite with transverse anterior sclerotised lobe (7, J)

RHYACOPHILIDAE except *Agapetus*.

7. Mesonotal sclerite divided into four. Gular sclerite trapezoidal in shape and completely divides genae (7, K). Larval case shield-shaped, formed of lateral wing-like extensions of the tubular centre. MOLANNIDAE.
 Mesonotal sclerite entire or divided into two sclerites only by a longitudinal suture 8.

8. Brush of hairs absent on inner (concave) side of right mandible LEPTOCERIDAE.

Brush of hairs present on inner (concave) side of right mandible 9.

9. Brush of hairs present on outer (convex) side of mandible BERAIDAE (*Beraeodes* only).

Brush of hairs absent from outer (convex) side of mandible
 BERAIDAE (*Beraea* only) and SERICOSTOMATIDAE (SERICOSTOMATINAE).

NOTE. In the absence of detailed studies of all the British species it is not possible to differentiate between *Beraea* and SERICOSTOMATINAE.

10. Metanotum entire or divided into 2 or 4 sclerites 11.
 Metanotum divided into 6 sclerites 12.
 11. Metanotum entire or divided into 2 sclerites only 13.
 Metanotum divided into 4 sclerites 14.

12. Four median sclerites very small, reduced to small patches, from each of which springs a single bristle (10, E). Clypeus with an additional excision on each side anteriorly (6, J). Genae with small inwardly directed lobes adjacent to gular sclerite (7, C). Larval case generally of quadrangular cross-section throughout its length

SERICOSTOMATIDAE (LEPIDOSTOMATINAE).

Four median sclerites each furnished with more than one bristle. Clypeus with a single lateral excision only. Inwardly directed lobes of genae adjacent to gular sclerite absent. Gular sclerite narrow or wide. Larval case never of quadrangular cross-section throughout its length 15.

13. Abdomen cylindrical and slender 16.

Abdomen thick, widest at about the fifth abdominal segment, whitish and dark spicules absent. Tufts of long black hairs on anal claspers absent. Length of larva up to 8 mm. Makes a hemispherical case of sand grains, small stones or diatoms, with both openings on the ventral surface, or of secretion only, seedlike with small amount of added matter 17.

14. Metanotum with two large parallel transverse sclerites, anterior sclerite of which is broad with posterior margin excised. Posterior sclerite narrow, thickened at the centre (10, I)

ODONTOCERIDAE (*Odontocerum albicorne* is only British representative).
 Metanotum without two large parallel transverse sclerites 18.

15. Gular sclerite narrow, widest at the centre and excised on lateral margins anteriorly (7, B). Mesonotum divided by longitudinal suture. Anterior projections of the lateral sclerites of the mesonotum (10, B)

LIMNOPHILIDAE.

Gular sclerite wide, widest at the anterior margin. Not excised on lateral margins (7, L). Mesonotum divided into 8 sclerites. Anterior projections of the lateral sclerites of the mesonotum present (10, C)

SERICOSTOMATIDAE (*Silo* in GOËRINAE).

16. Tufts of long black stiff hairs present on anal claspers (14, D). Body dark greyish or greyish-brown covered with dark coloured spicules, legs short (3). Length of larva 10 mm.-20 mm. Do not bear a movable larval case but inhabit a fixed case adjacent to a small silken net attached to small stones or vegetable debris HYDROPSYCHIDAE.

Tufts of long black stiff hairs on anal claspers absent. Mentum very wide, ligula acute PSYCHOMYIDAE (*Ecnomus* only).

17. Legs long, metanotal sclerites restricted to small patches more or less distinct. Case of sand grains, etc., hemispherical with both openings on ventral surface. Larva is eruciform type. Relative size of abdomen to thorax normal. Length of larva up to 9 mm. RHYACOPHILIDAE (*Agapetus*).
 Legs short, metanotal sclerites large. Case sometimes seedlike, often with rounded ends forming lateral shields to the openings. Larva is campo-deiform type. Abdomen relatively large to size of thorax. Length of larva up to 7 mm. HYDROPTILIDAE.
18. Metanotal sclerites in two groups of two. Mesonotum of four sclerites, the outer of which are triangular with heavily sclerotised black projections outwardly directed. Head strongly retractile into pronotum, the latter furnished with wing-like anterior lateral projections (10, D). Posterior margin of pronotum not strongly excised
 SERICOSTOMATIDAE (*Goëra* only in GOËRINAE).
 Metanotal sclerites grouped in arc with concavity directed anteriorly. Mesonotal sclerites four in number, quadrangular and transverse. Posterior margin of pronotum strongly excised (10, O)
 SERICOSTOMATIDAE (BRACHYCENTRINAE).

REFERENCES.

The most important works which have been consulted are listed here, but for an almost complete list of references on Trichoptera the reader is referred to Betten's *Caddis Flies of New York State*. The references given in List 1 are to works dealing solely with British specimens. In List 2 are given references to other works. In general the references given are restricted to publications giving some account, or some figures, of the larvae of Trichoptera.

LIST 1.

REFERENCES TO PUBLICATIONS DEALING WITH THE BRITISH SPECIES.

HICKIN, N. E., 1942-1944. *Larvae of the British Trichoptera*.

1. *Stenophylax stellatus* Curtis. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 9-11.
2. *Trianodes bicolor* Curtis. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 12-13.
3. *Rhyacophila dorsalis* Curtis. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 14-16.
4. *Philopotamus montanus* Donovan. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 16-17.
5. *Odontocerum albicorne* Scopoli. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 119-22.
6. *Silo pallipes* Fabricius. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 123-6.
7. *Phryganea grandis* L. 1942, *Proc. R. ent. Soc. Lond.* (A) 17 : 134-7.
8. *Limnophilus flavicornis* L. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 6-10.
9. *Anabolia nervosa* Curtis. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 11-14.
10. *Lepidostoma hirtum* Fabricius. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 15-17.
11. *Holocentropus dubius* Rambur. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 19-21.
12. *Limnophilus lunatus* Curtis. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 66-8.
13. *Mystacides nigra* L. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 69-71.
14. *Limnophilus vittatus* Fabricius. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 72-4.
15. *Goëra pilosa* Fabricius. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 75-7.
16. *Agapetus fuscipes* Curtis. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 78-80.
17. *Brachycentrus subnubilus* Curtis. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 81-3.
18. *Leptocerus aterrimus* Stephens. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 106-8.
19. *Setodes argentipunctella* McLachlan. 1943, *Proc. R. ent. Soc. Lond.* (A) 18 : 109-11.
20. *Neuronina ruficrus* Scopoli. 1944, *Proc. R. ent. Soc. Lond.* (A) 19 : 12.

- KIMMINS, D. E., 1943, A note on the Caddis Fly, *Mystrophora intermedia* Klapálek (Trichoptera). *Proc. R. ent. Soc. Lond. (A)* 18 : 96-8.
- MIALL, L. C., 1905, *The Natural History of Aquatic Insects*.
- MORTON, K. J. This author contributed a large number of papers on Trichoptera from 1883 to 1930, many of them containing descriptions of the immature stages. A small selection of these papers is given here.
- , 1884, On the Larva, etc. of *Beraeodes minuta* L. *Ent. mon. Mag.* 21 : 125-6.
- , 1888, The Larva and Case of *Ithytrichia lamellaris* Eaton, with references to other species of HYDROPTILIDAE. *Ent. mon. Mag.* 24 : 171-5.
- , 1888, The Larva etc. of *Philopotamus*. *Ent. mon. Mag.* 25 : 89.
- , 1890, Notes on the Metamorphoses of Two Species of the Genus *Tinodes*. *Ent. mon. Mag.* (2) 1 : 38-42.
- , 1890, Notes on the Metamorphoses of British LEPTOCERIDAE. *Ent. mon. Mag.* 26 : 127-31, 181-4, 231-6.
- , 1904, The Preparatory Stages of *Adicella filicornis* Pict. *Ent. mon. Mag.* (2) 15 : 82-4.
- MOSELY, M. E., 1921, *The Dry-Fly Fisherman's Entomology*.
- , 1926, *Insect Life and the Management of a Trout Fishery*.
- , 1939, *The British Caddis Flies*.

LIST 2.

The following references give a review of the literature on the immature stages of Trichoptera from sources other than British.

- BETTEN, C., 1934 (with chapters by B. L. Kjellgren, A. W. Orcutt and M. B. Davis). The Caddis Flies or Trichoptera of New York State. *Bull. N.Y. St. Mus.* No. 292.
- ESBEN-PETERSEN, P., 1916, *Vaarfluer, Danmarks Fauna*, 19.
- HAGEN, H. A. This author was responsible from 1851-87 for a large number of papers on Trichoptera, including the immature stages. The material described was collected from all parts of the world.
- , 1866, Description of a genus of caddis flies, of which the larvae construct cases, known as *Helicopsyche*. *Ent. mon. Mag.* 2 : 252-5.
- KLAPÁLEK, F. Much of our knowledge of the Trichoptera and their systematics is due to the work of this author, who published from 1888 to 1913 a series of papers dealing mainly with Hungarian and Balkan species.
- , 1889, The Metamorphoses of *Apatania muliebris* McLach., a chapter in Parthenogenesis. *Ent. mon. Mag.* 25 : 241-2.
- KRAFKA, J., 1915, A key to the Families of Trichopterous Larvae. *Canad. Ent.* 47 : 217-22.
- LESTAGE, J. A., 1921, Trichoptera in Rousseau : *Les Larves et Nymphes Aquatiques des Insectes d'Europe*.
- MCLACHLAN, R., Over a period of more than forty years (1862-1903) McLachlan contributed to the literature of the Trichoptera. His best-known work is given below.
- , 1874, *A Monographic Revision and Synopsis of the Trichoptera of the European Fauna*. Pt. 1. Further parts and supplements published in 1874, 1875, 1876, 1877, 1878, 1879, 1880 and 1884.
- MARTYNOV, A. B. This author wrote mainly on Russian species and most of his papers are in Russian.
- ROSS, H. H., 1944, The Caddis Flies, or Trichoptera of Illinois. *Bull. Ill. nat. Hist. Surv.* 23 : 1.
- ROUSSEAU, E., 1921, (the chapter on Trichoptera is the work of Lestage) *Larves et Nymphes Aquatiques des Insectes d'Europe*.

SCHWANWITSCH, B. N., 1943, *Nature* 152 : 727.

SILFVENIUS, A. J. (SILTALA). Numerous papers were published from 1900 to 1908 on the metamorphoses of Trichoptera mainly in *Acta Soc. Fauna Flora fenn.*, or *Medd. Soc. Fauna Flora fenn.* (Note. The author's change of name from Silfvenius to Siltala took place in 1906.)

SNODGRASS, R. E., 1935, *Principles of Insect Morphology*.

ULMER, G. The work of this author has already been referred to in the text. Much of his work is collected together in the following two works.

—, 1903, Über die Metamorphose der Trichoptera. *Abh. Naturw. Ver. Hamburg* 18 : 1-154.

—, 1909, Trichoptera in *Süsswasserfauna Deutschlands* 5-6.

WESENBERG-LUND, C. J. This author wrote a number of papers on the biology of Caddis larvae from 1908 to 1915 mainly in *Int. Rev. Hydrobiol.* The following paper is selected.

—, 1911, Biologische Studien über Netzspinnen der Campodeoide Trichopteren-larven. *Int. Rev. Hydrobiol. (Biol. suppl. 3)* 4 : 1-64.

ERRATA.

Proc. R. ent. Soc. Lond. (A) 17.

Page 9, line 19, For *Stenophyllax* read "*Stenophylax*".

Page 11, line 20, For "trochanter" read "coxa".

line 21, Read "In all legs there are two distal spurs on tibia and tarsus and two marginal spurs on the femur".

Page 16, line 5, For "proximal tarsal segment" read "tibia".

line 6, For "tibia" read "femur".

Page 122, line 11, For "Femur and tibia" read "coxa and femur".

Page 135, line 22, For "tibia" read "femur".

line 24, For "present on the tarsus" read "present on the tibia and tarsus".

Page 136, line 2, For "femur" read "coxa".

Proc. R. ent. Soc. Lond. (A) 18.

Page 67, Text-figures Nos. 6 and 9 have become transposed.

Vol. 97. Part 9. Pp. 213-235, 5 figs.

21st October, 1946.

INST. ENT.
LIBRARY

22 OCT 1946

THE

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

X GEIJSKES, D. C. Observations on the Odonata of Tobago, B.W.I.	PAGE 213-235, 5 figs.
--	--------------------------

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D. }

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (Chairman).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAFT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (Chairman).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (Chairman).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (Secretary).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (Chairman).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939.

Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

OBSERVATIONS ON THE ODONATA OF TOBAGO, B.W.I.

By D. C. GEIJSKES.

(Entomologist, Agricultural Experiment Station, Paramaribo, Surinam.)

Communicated by E. McC. Callan.

Manuscript received 8th November, 1945.

(Read 5th June, 1946.)

WITH 5 TEXT-FIGURES.

CONTENTS.

	PAGE
Introduction	213
2. General information	213
3. Limnology	214
4. The species and the collecting places	215
5. Ecology	216
6. Geography	217
7. Systematic Account of the Imagines	219
8. Nymphs	223
9. Literature cited	234

NOTHING is known about the Odonata of the island of Tobago. In October 1944, the author visited this pretty island on a holiday trip, and during this visit some collecting was done, mostly in the flat south-western part of the island, as very little could be undertaken in the mountains because of the difficulty of travel.

A total of 143 imagines was collected, but nymph-dredging was carried out only in a creek on Orange Hill Road; some exuviae were picked up in other places. Although it is evident that this account cannot be complete, some information about the principal species and the ecological and geographical relations of the Odonata of the island is outlined in what follows.

2. GENERAL INFORMATION.¹

Tobago is an island having an area of some 114 square miles and lies in the Atlantic Ocean separated about 26 miles from the north-eastern point of Trinidad, between the latter island and Barbados and Grenada, southernmost of the Lesser Antilles. It is situated at 60° 40' W. and 11° 15' N. Structurally it is not related to the Antilles, but is in agreement with the neighbouring portion of the South American continent and is therefore mountainous with a central east-west backbone. The island itself is 26 miles in length and 7½ miles broad at its widest point, being roughly elliptical in shape. The mountain backbone known as the Main Ridge makes a small angle with the axis of the island, and is some 10 miles long, rising abruptly at either end. The highest point of the Main Ridge touches 1890 feet, but not in any well-defined peak,

¹ In a recent publication, Dr. J. S. Beard (1944) has brought together much data of importance for ecological studies and the following information is obtained from this source.

the crest running as a ridge about 1600 to 1700 feet high throughout. Much of this ridge is covered with forest. The adjacent country is all steeply broken land and there is no coastal plain except at the south-western extremity, where the country gradually evens off to form a flat plain known as the lowlands, some 10 square miles in area. Topography in general is young, and drainage is by swift-flowing torrents rising in the Main Ridge.

The average rainfall varies from 56 inches in the south-west to 93 inches in the north-east. All the stations reveal a similar rainfall, characteristically divided into a dry and a wet season, the former from January to May and the latter from June to December. Climatically, Tobago belongs to the Lesser Antilles.

Tobago lies on the same continental shelf which also carries Trinidad, being separated from the latter island by relatively shallow water, whereas deeps of several hundred fathoms divide it from Barbados and Grenada.

The mountains of Tobago constitute the last and most easterly link in the great coastal cordillera of Venezuela. Tobago, the Northern Range of Trinidad, and the Paria Peninsula of Venezuela, are three ridges of related structure arranged parallel and "en echelon." The whole of the island north of a line running roughly parallel to, and about a mile south of, the Main Ridge, is formed of metamorphic rocks of sedimentary origin consisting chiefly of schistose grits, often very felspathic with talcose and talc mica schists. These resemble in a general degree strata in the Northern Range of Trinidad, and are most likely of similar age: that is, lower cretaceous; but limestones are totally absent and quartz veins relatively rare.

The flat plain of the lowlands is composed of Tertiary and Quaternary beds, mainly coral limestones which rise in a series of flat terraces. The remainder of the island is formed of a mass of basic igneous rock which has shared the metamorphism of the schists and grits, and is highly shattered. During the Oligocene period, Tobago probably formed part of the continent, but was separated by submergences during the Miocene. In Pliocene times it is probable that Tobago was once more united with the mainland, only to become detached again soon afterwards. Tobago has now probably led a separate existence for at least 500,000 years.

3. LIMNOLOGY.

From a limnological point of view, Tobago offers two main types: streams and swamps, the former predominating throughout the island, forming the drainage system of the mountainous Main Ridge. The streams flow down the mountains often through deep and steep valleys, whereas their course is limited in the more flattened coastland before reaching the ocean. They all belong to the mountainous stream type, very rocky in the upper part, often with some waterfalls, and in the lower course with a bed of pebbles and sand, sometimes muddy in the last stretch near their outlet into the ocean. Normally in every stream we may distinguish an upper-, middle-, and lower-course, but in those places where the mountains approach the ocean, the lower course is absent and the middle course runs directly into the ocean (Doctor's River in Speyside and probably some other creeks on the north coast of the island).

In the mountains the rivers are surrounded by a natural forest, in cultivated places mostly by cacao plantations and bamboo, while in the plains they run in open country, for the most part bordered by bamboo and shrubs. The water of these streams is clear, but during rainy weather or a short time after

heavy showers it is muddy. Neither chemical nor physical data from these natural waters are available at present.

The swamps are secondary in importance and only present in the lowlands in the south-western part of the island. Here we find some lagoons along the coast in the youngest deposits outside the coral terraces. All these swamps are under the influence of salt water from the open ocean nearby and this brackish effect is well demonstrated by the presence of mangrove woodland around the swamp-pools, while the swamp itself is commonly covered with a stiff salt-water grass.

Sometimes the lower courses of creeks running through the lowlands are partly dried up and reduced to several standing pools in the deepest places of their bed, but this is a temporary condition. More often the mouths of the rivers are dammed up by a sand bar on the beach, with the result that the creek water is backed up to form a stagnant pool for some distance behind that barrier. The only permanent freshwater pool visited was a small artificial pool overgrown with waterlilies in the Botanic Garden in Scarborough.

4. THE SPECIES AND THE COLLECTING PLACES.

The following species of Odonata are now recognised for Tobago :—

- | | |
|--|--|
| 1. <i>Hetaerina macropus</i> Selys. | 10. <i>Micrathyria aequalis</i> Hagen. |
| 2. <i>Argia translata</i> Selys. | 11. <i>Erythrodiplax umbrata</i> L. |
| 3. „ <i>difficilis</i> Selys. | 12. <i>Erythrodiplax ochracea ochracea</i> |
| 4. „ <i>orichalcea</i> Hagen. | (Burmeister) Ris. |
| 5. <i>Ischnura ramburi</i> var. <i>credula</i> | 13. <i>Erythrodiplax connata fusca</i> |
| Hagen. | (Rambur) Ris. |
| 6. <i>Gynacantha nervosa</i> Rambur. | 14. <i>Erythemis plebeja</i> Burmeister. |
| 7. <i>Orthemis ferruginea</i> Fabricius. | 15. <i>Lepthemis vesiculosa</i> Fabricius. |
| 8. <i>Micrathyria didyma didyma</i> | 16. <i>Dythemis sterilis</i> Hagen. |
| (Selys) Ris. | 17. <i>Pantala flavescens</i> Fabricius. |
| 9. „ <i>ocellata dentiens</i> Calvert. | 18. <i>Tramea cophysa</i> Hagen. |

Odonata were collected in the undermentioned localities on the island (from west to east) :—

Pigeon Point. Near this spot on the south-west point of the island there is one of the largest swamps, surrounded by shrubs and cacao plantations. The water seems to be at least partly brackish, as indicated by typical salt-water plants such as *Avicennia*, *Laguncularia*, and a stiff swamp-grass probably *Sporobolus*, growing in and covering a good deal of the open water. Here eleven species were collected (Nos. 5, 7, 8, 9, 10, 11, 12, 14, 15, 16, 18).

Store Bay or Milford Bay. Beside the beach itself, below the coral rocks, there are some open places in cultivated land near the airport on a coral terrace. Some of the common species encountered in the swamp of Pigeon Point are met with here again (Nos. 7, 11, 18).

Mount Irvine or Little Courland Bay. Along this coconut beach and in the hilly country behind, only the most common species (No. 11) was found.

Milford Road. On two streamlets in a cacao estate three species were taken (Nos. 2, 5, 16).

Lambeau River. This river formed the main collecting place a few miles west of Scarborough. It finds its origin in several tributaries running down from the hills around the Orange Hill Road (590 feet) and flows through lowland

bordered mostly by bamboo to the sea east of the village of Lambeau. Fifteen of the eighteen known species of the island are found in and around this stream (Nos. 1, 2, 4, 5, 6, 7, 10, 11, 12, 13, 14, 15, 16, 17, 18).

Orange Hill Road. The creeks running down the hills through cacao estates and cultivated country form the upper part of the Lambeau River. Here seven species were encountered (Nos. 1, 2, 3, 4, 7, 13, 16).

Rockly Vale and Botanic Garden near Scarborough. Some springlets and an artificial pond in the Botanic Garden in Scarborough produced only seven species (Nos. 2, 7, 9, 10, 11, 13, 16).

Craig Hall Falls near Mason Hall. This is a very picturesque fall on one of the upper streams of the Courland River, running down from the west slopes of the Main Ridge, and was the only mountainous spot visited in the island. In spite of this, only three species of dragonflies were observed (Nos. 1, 2 and 3).

Speyside Doctor's River. Along the standing outlet of this river into Speyside Bay seven species were collected (Nos. 7, 10, 11, 12, 13, 14, 18), while in its mountainous middle course, along the road to Charlotteville, only one species (No. 1) was observed. Probably the rainy weather conditions, under which this trip was made, were partly responsible for this poor result.

5. ECOLOGY.

In the following statement the species of Odonata are tabulated under four kinds of habitat. The first three belong to the lotic (running water) environment, in which we must distinguish between an upper, a middle, and a lower course of the river system; the fourth represents the lentic (standing water) environment; i.e. the lagoon or coast swamp.

TABLE 1.

Ecological distribution of the species of Odonata on the island of Tobago.

	Lotic environment			Lentic environment
	River upper course.	River middle course.	River lower course.	Swamp
<i>Hetaerina macropus</i>	×	×	×	
<i>Argia translata</i>	×	×	×	
" <i>difficilis</i>	×	×		
" <i>orichalcea</i>		×	×	
<i>Ischnura ramburi credula</i>			×	×
<i>Gynacantha nervosa</i>			×	
<i>Orthemis ferruginea</i>		×	×	×
<i>Micrathyria didyma didyma</i>			×	×
" <i>ocellata dentiens</i>			×	×
" <i>aequalis</i>			×	×
<i>Erythrodiplax umbrata</i>			×	×
" <i>ochracea ochracea</i>			×	×
" <i>connata fusca</i>			×	
<i>Erythemis plebeja</i>			×	×
<i>Lepthemis vesiculosa</i>			×	×
<i>Dythemis sterilis</i>		×	×	×
<i>Pantala flavescens</i>			×	×
<i>Tramea cophysa</i>			×	×
	3	6	16	12

From Table 1 the following peculiarities are apparent: the species living in the running water are recognisable from those living in the lentic environment. In the first category we may reckon: *Hetaerina macropus* and the three species of *Argia*, for they have not been found outside the rivers. *Dythemis sterilis* is somewhat doubtful in this respect, as it has been found also in the swamp, although other species of this genus are typical stream dwellers. It seems that this species descends from the rivers into the swamp, transferring from the lotic to the lentic environment.

The other species, thirteen in number, all belong to the lentic group. This is surprising, for in this country the lotic environment is much more represented than the lentic. This can be partially explained by the fact that the lotic species are much more limited in their environment than are the lentic, which is demonstrated also in their geographical distribution.

The lotic species may be regarded more or less as relics, living in isolation in the mountainous streams, at least as long as the land-mass itself has been separated from the continent. The lentic species, however, represent the younger elements in the fauna. They migrate from standing waters partly into the lotic environment, viz. the lower course of the rivers, and sometimes into the middle course, as in the case of *Orthemis*. Most of the lentic species are strong fliers, able to cover long distances even over the ocean (*Pantala*, *Tramea*, *Orthemis*, *Lepthemis*, *Gynacantha*). It seems therefore likely that in this group of species the elements partly immigrated from the neighbouring countries after the separation of the island from the continent took place. Moreover, many species among them are able to breed in brackish water (*Ischnura ramburi*, *Orthemis ferruginea*, *Micrathyria aequalis*, *Erythrodiplax umbrata*, *Erythemis plebeja*, *Lepthemis vesiculosa*, *Pantala flavescens* and *Tramea cophysa*), which fact partly explains also their wide distribution and their common occurrence all along the coasts of the neotropical region.

Furthermore, most of the species are to be found in the lower courses of the rivers (sixteen species out of a total of eighteen), whereas six species live in the middle course and three species in the upper course, while twelve species inhabit the swamps. This phenomenon is explained by the fact that the fauna of the lower courses of the rivers forms a mixture of both lotic and lentic species. Here the two categories meet one another.

Finally we have to note the isolated position of *Gynacantha nervosa* and *Erythrodiplax connata fusca*, belonging to the species living in the lentic environment but so far not observed in the swamps, while *Micrathyria didyma didyma* is found in the swamp only. How far these aberrant features are the result of our incomplete knowledge should be explained by further work.

6. GEOGRAPHY.

In the following statement (Table 2) the species of Odonata, now recognised in the island of Tobago, are tabulated together with their distribution among the other countries of the Caribbean area.

From this table it is clear that the dragonfly fauna of Tobago is closely related to that of Trinidad and of the continent of South America (especially the North-western part, viz. Venezuela and Colombia). Furthermore, there is no great difference from the dragonfly fauna of Central America, where, as Calvert (1908) points out, "the South American element is much the strongest." The Greater Antillean islands have still much in common with the latter, whereas the Lesser Antilles, although the nearest neighbours of Tobago, show only a

TABLE 2.

Geographical distribution of the species of Odonata of the island of Tobago.

Tobago	Trini- dad	Northern S. America	Central America	Greater Antilles	Lesser Antilles
1. <i>Hetaerina macropus</i> . . .	×	×	×		
2. <i>Argia translata</i> . . .	×	×	×		
3. „ <i>difficilis</i> . . .	×	×	×		
4. „ <i>orichalcea</i> . . .	×	×	×		
5. <i>Ischnura ramburi</i> var. <i>credula</i>	×	×	×	×	×
6. <i>Gynacantha nervosa</i> . . .	×	×	×	×	
7. <i>Orthemis ferruginea</i> . . .	×	×	×	×	×
8. <i>Micrathyria didyma didyma</i> .	×	×	×	×	×
9. „ <i>ocellata dentiens</i>	×	×			
10. „ <i>aequalis</i> . . .	×	×	×	×	×
11. <i>Erythrodiplax umbrata</i> . . .	×	×	×	×	×
12. „ <i>ochracea ochracea</i>	×	×	×	×	
13. „ <i>connata fusca</i> . . .	×	×	×		
14. <i>Erythemis plebeja</i> . . .	×	×	×	×	
15. <i>Lepthemis vesiculosa</i> . . .	×	×	×	×	×
16. <i>Dythemis sterilis</i> . . .	×	×	×		×
17. <i>Pantala flavescens</i> . . .	×	×	×	×	×
18. <i>Tramea cophysa</i> . . .	×	×	×	×	
	18	18	17	11	8

slight affinity. From this analysis we may consider a more direct relation of the dragonfly fauna of Tobago to that of northern South America, than to that of the Antillean islands. This is not surprising and well in agreement with some other features of both the fauna and the flora of Tobago.

Furthermore all the known species from Tobago are without exception known also in Trinidad, which in its origin is continental (Williamson 1923, Geijskes 1931 and 1932). But on the other hand many species occurring in Trinidad have not yet been found in Tobago and probably will never be encountered there. Of the 92 species known from Trinidad only 18 are recorded from Tobago, distributed among the families as follows:—

	Trinidad	Tobago
AGRIONIDAE	2	1
LESTIDAE	2	—
COENAGRIONIDAE	22	4
GOMPHIDAE	2	—
AESCHNIDAE	12	1
LIBELLULIDAE	52	12
	92	18

Within the class Insecta, attention may be called to the butterflies, the termites and the Anophelines, which as far as is known to the author are the only other groups of insects more particularly recorded for Tobago.

Lamont (1917) records 51 species of butterflies for Tobago, saying that: "this number could doubtless be largely increased by systematic collection throughout the island at different seasons of the year. But I doubt whether it will ever exceed, or even reach, 100. In Trinidad 500 is by no means an impossible ideal. Almost 450 species have already been recorded."

Adamson (1940) listed 56 species of termites for Trinidad, of which 10 occur in Tobago.

Downs, Gillette and Shannon (1943), in their report on a malaria survey of Trinidad and Tobago, mention thirteen species of Anophelines in Trinidad, of which three are found in Tobago.

We may therefore tabulate the proportion of the species of the mentioned insect groups for Trinidad and Tobago as follows:—

	Trinidad	Tobago	
Lepidoptera	450	51	(11%)
Isoptera	56	10	(18%)
ANOPHELINEAE	13	3	(23%)
Odonata	92	18	(19%)

Not all the species occurring in Tobago occur also in Trinidad. Lamont remarks of the butterflies of Tobago: "I took another *Euptychia* which I have not hitherto seen in Trinidad, or yet identified; and also a *Heliconius*, of the usual red-and-black appearance, but differing from the species (*H. hydara*) so abundant in Trinidad in its very much narrower scarlet band."

Belcher (1939), discussing the avifauna of Tobago (in Alford's *Tobago Guide Book*), says: "Its birds to-day are South American, and in general are represented by the same or very nearly allied forms on the Continent. What may well surprise the visitor is that there should be so many kinds common in Trinidad which do not occur at all in Tobago,² while Tobago can show at least eight birds not found in its larger sister island." And again: "Tobago's commonest Woodpecker is a bird unknown in Trinidad, though curiously enough it crops up again on Patos, Trinidad's westernmost dependency close in to the Venezuelan shore."

The same observation is made by Beard (1944) for the flora of which he says: "Several species belonging to the mainland occur abundantly in Tobago but in Trinidad are absent or exceedingly rare. Similarly several species abundant in the Northern Range of Trinidad are almost absent from Tobago."

These facts seem to indicate that originally the fauna and flora of Tobago came directly from some part of the Venezuelan coast north-west of the Bocas, and not via Trinidad, which received its living elements, probably, from a more southern part of Venezuela. That this indication is not visible at present in the record of the Odonata (and probably in other aquatic animals) may find its reason in incomplete exploration, or in the limited ecological conditions in Tobago. It will therefore not be surprising to meet with analogous relations, especially in terrestrial animals, as found now in the plants, the birds and the butterflies, by further exploration of the island. Also a more complete knowledge of the eastern part of Venezuela will be necessary and helpful in solving these problems.

7. SYSTEMATIC ACCOUNT OF THE IMAGINES.

1. *Hetaerina macropus* Selys.

Lambeau River, near Gov. Farm, 5 Oct., 1 ♂, 3 ♀.

Orange Hill Road Creek, in cocoa estate, 14 Oct., 2 ♂, 2 ♀.

Open pools in springlet along Road, 23 Oct., 1 ♂, 1 ♀.

Speyside, Doctor's River, 29 Oct., 1 ♂.

² For example, the well-known Kiskadee (*Pitangus sulphuratus* L.).

2. *Argia translata* Selys.

Milford Road, creek in cocoa estate, 27 Oct., 2 ♂.

Gov. Farm Road, springlet with small pools, 14 Oct., 1 ♂, 1 ♀.

Orange Hill Road, springlet with small open pools, 23 Oct., 2 ♂.

Creek in cocoa estate, 14 Oct., 5 ♂, 2 ♀.

Lambeau River, near Gov. Farm, 5 Oct., 6 ♂, 5 ♀.

Scarborough, Bot. Gard. springlet, 29 Sept., 1 ♂.

Mason Hall, Craig Hall Falls, 2 Oct., 4 ♂, 2 ♀ (one pair in oviposition).

Males with black labrum and with black last abdominal segments. In the structure of the male appendages and in the form of the female mesothoracic laminae the specimens agree with the Central and South American material.

On rivers, creeks and in open springlets in the mountains *translata* is the most common *Argia* species; when alive the black mature males are conspicuous by their violet eyes.

3. *Argia difficilis* Selys.

Orange Hill Road, creek in cocoa estate, 14, 21, 23 Oct., 8 ♂, 2 ♀.

Mason Hall, Craig Hall Falls, 2 Oct., 1 ♂.

This lovely marine blue-coloured species was met with in small numbers together with the other two species of *Argia*, settling on stones and on leaves in sunny spots. It prefers springlets to larger creeks. The specimens agree with material from Trinidad and Surinam but their real systematic position is not yet clear, for the Selys species of "*difficilis*" form a problem by itself.

4. *Argia orichalcea* Hagen.

Orange Hill Road, creek in cocoa estate, 14 Oct., 3 ♂, 2 ♀.

Lambeau River, near Gov. Farm, 12 Oct., 1 ♂.

This beautiful coloured species, with the copper shining thorax and the red eyes in the male sex, was common in a creek crossing the Orange Hill Road near Scarborough. Oviposition was observed among leaves and material washed ashore between stones in sunlit places. The species fully agrees with specimens from Trinidad which, after the descriptions of Ris (1918), agree better with *orichalcea* than with *cuprea*.

5. *Ischnura ramburi* Selys var. *credula* Hagen.

Lambeau River, near Gov. Farm, 5 Oct., 1 ♂, 4 ♀.

Milford Road, small creek in cocoa estate, 27 Oct., 1 ♂.

Pigeon Point, swamp, Oct., common.

Most of the males belong to the var. *credula* Hagen, having their abdominal segment 9 blue with the black reduced to an apical spot, or the middorsal black stripe reduced to a small basal and a larger apical spot reaching to half the segment length. In a few specimens the two spots are connected by a narrow black stripe (*ramburi* type). In one of the females the vulvar spine is wanting.

In Tobago this species is common along the sea-coast in swamps and in the lower courses of the rivers in the flat south-western part of the island.

6. *Gynacantha nervosa* Rambur.

Gov. Farm Road, in twilight, 12 Oct., 2 ♂.

In mosquito-trap near Lambeau, 16 Oct., 1 ♀.

The large dull brown-coloured species was often observed in the twilight

soaring along the roads. The species agrees in detail with specimens from Surinam.

7. *Orthemis ferruginea* Fabricius.

Pigeon Point, swamp, 8 Oct., 3 ♂.

Store Bay, 11 Oct., 1 ♂.

Lambeau River, 12 Oct., 1 ♂.

Speyside, Doctor's River, common (observed).

The specimens examined are undoubtedly *ferruginea* with four rows of cells in the hind-wing between A_3 and the hind margin at the level of the hind angle of the triangle. Pterostigma 5.5–6 mm., wing tips smoky. In adults the paler stripes on thorax faded and reduced to a lower spot of the third band just before the stigma and to the lower half of the sixth band on metepisternum. In several males the six paler bands on the sides of the thorax easily visible, although not so sharply developed as in the females. Legs dark brown to black. By these markings the examples belong rather to the subspecies *sulphurata* Hagen than to the typical *ferruginea* Fabr. Male abdomen 31–32 mm., hind-wing 39–40 mm.

The species is common throughout the island, especially in the swamps along the sea-coast, over creek mouths and in the lower courses of the rivers. The adult males attract attention by their brilliant purple red-coloured abdomen and thorax.

8. *Micrathyria didyma didyma* (Selys) Ris.

Pigeon Point, 8 Oct., 1 ♂ ad., 1 ♀ juv.

According to wing-venation and thorax colour pattern this is typical *didyma* subspecies. Male abdomen 24 mm., hind-wing 27 mm., pterostigma 2.5 mm.; female abdomen 22 mm., hind-wing 27 mm., pterostigma 2.5 mm.

9. *Micrathyria ocellata dentiens* Calvert.

Scarborough, Bot. Gard., small pool with waterlilies, 29 Sept., 1 ♂ (*in copula* with a female of *Micr. aequalis*!).

The specimen shows the dark coloured pattern scheme on sides of thorax (cf. Geijskes 1932). Abdomen ♂ 22 mm., hind-wing 24 mm., pterostigma 2.5 mm.

10. *Micrathyria aequalis* Hagen.

Pigeon Point, swamp, 8 Oct., 4 ♂, 3 ♀ juv.; 22 Oct., 1 ♂ juv.

Lambeau River, near Gov. Farm 12 Oct., 2 ♂ ad.

Scarborough, Bot. Gard., 29 Sept., ♂♀ *in coitu*.

Speyside, Doctor's River mouth, 30 Oct., 1 ♂.

The specimens show some anomalies in the wing-venation: *ti* in front-wing 3.3, 2.3, 2.2 celled; *t* in front-wing (right side) with one cross vein (one specimen from Speyside). The specimen from Speyside is nearly black, slightly pruinose and with the yellow spots on abdominal segment 7 conspicuous, covering more than the first half of the segment.

11. *Erythrodiplax umbrata* L.

Pigeon Point, swamp, Oct., common.

Storebay, 11 Oct., 1 ♂.

Irvingbay, 6 Oct., 2 ♂.

Lambeau River, near Gov. Farm, 5, 12 Oct., 2 ♂, 3 ♀.

Scarborough, Bot. Gard., 29 Sept., 1 ♂.

Adult males with the dark brown wing-band reaching from the nodus to the stigma, or (in the specimen from Storebay) to the proximal third of stigma. In the females only the heterochromatic form with the hyaline yellowish-tinged and brown-tipped wings is present.

A common species in the lowlands on marshy places and along springlets in cocoa gardens, grass-fields etc.

12. *Erythrodiplox ochracea ochracea* (Burmeister) Ris.

Pigeon Point, swamp, 8, 15, 22 Oct., 5 ♂, 2 ♀.

Lambeau River, near Gov. Farm (springlet), 5 Oct., 1 ♂ ad.

Speyside, mouth of Doctor's River, 29 Oct. (observed).

It is the typical *ochracea*-form with the large red-brown wing-spot and with the characteristic male genital armature.

It is found in several places in the lowlands along springlets and in swampy places near the coast.

13. *Erythrodiplox connata fusca* (Rambur) Ris.

Lambeau River, near Gov. Farm, 5, 14 Oct., 2 ♂ ad.

Orange Hill Road, small open pools in the hills, 23 Oct., 1 ♂, 1 ♀.

Scarborough, Bot. Gard., pool with waterlilies, 29 Sept., 2 ♂.

Speyside, mouth of Doctor's River, 30 Oct., 1 ♂.

Located on springlets, pools and rivers etc. in open grassy places.

14. *Erythemis plebeja* Burmeister.

Lambeau River, near Gov. Farm, 12 Oct., 1 ♂.

Pigeon Point, 15 Oct. (observed).

In the flat south-western part of the island on swampy places and along the rivers. The species is not commonly met with and only a few adult black individuals were observed.

15. *Leptemis vesiculosa* Fabricius.

Pigeon Point, swamp, 22 Oct., 1 ♂ and a few others observed.

Lambeau River, near Gov. Farm, Oct. (observed).

This fine green yellow and black species is not frequently seen and occurs in the same places as the foregoing species.

16. *Dythemis sterilis* Hagen.

Pigeon Point, swamp, 8 Oct., 1 ♂.

Milford Road, creek in cocoa garden, 27 Oct., 1 ♂.

Lambeau River, lower part, 5, 12 Oct., 2 ♂ ad.

Orange Hill Road, springlets and pools, 14 and 23 Oct., 2 ♂; creek in cocoa-estate, 21 Oct. (nymphs).

Scarborough, Bot. Gard., along springlet, 29 Sept., 1 ♂.

In comparison with the Trinidad specimens, the Tobago examples are of a smaller size, male abdomen 25-28 mm., hind-wing 26-28.5 mm., pterostigma 2.5-3 mm. The yellow dorso-lateral spots on abdominal segment 6 and 7 sometimes shorter than half the segment length.

Common on small rivers and on springlets in the western part of the island; found also in the brackish water of Pigeon Point.

17. *Pantala flavescens* Fabricius.

Scarborough near Lambeau River on open grass-land and over the mouths of creeks near the beach, Oct., 2 ♀.

A common species along the sea-coast and on open grass-land in the south-western part of the island. The species mostly flies together with *Tramea cophysa*, soaring behind trees and shrubs for hours without settling, especially in the afternoon, and catching small insects.

18. *Tramea cophysa* Hagen.

Scarborough near Lambeau River on open grass-field, 1 ♀.

Pigeon Point and Storebay (observed).

The female collected belongs to the form *a* of Ris (*Libellulinen*, Cat. Coll. Selys Longchamps XVI, le 1913) which probably represents the *longicauda* var. of Calvert (*B.C.A.* 1906) or *calverti* of Muttkowski (1910, *Bull. Publ. Mus. Milwaukee* 1 : 1, cited after Ris).

Living in the same places as the foregoing species and mostly more abundant and outnumbering *Pantala* when flying together.

8. NYMPHS.

Hetaerina macropus Selys, fig. 1.

There is some doubt as to my identification of this nymph. In its general appearance it closely resembles those of the other species of *Hetaerina*, as far as they are known. The particular details are as follows :—

Head dotted irregularly, the marks more or less distinctly arranged in two rows on each half, one along the inner eye margin and another one along the median line. Occipital border moderately excavated in the middle, the hind lobes somewhat toothed. *Antenna* seven jointed, the long first segment in the basal half dark brown, with a black ring to the apical end and along the inner side a row of small and not very distinct setae (see Plate 1, B). Segm. 2 darkened in the basal half, segm. 3 with a distinct black ring at base. Relative length of the segments 147 : 40 : 29 : 16 : 9 : 8 : 8. *Mentum* (Plate 1, E) long, broadly spoon-shaped and dilated in its apical half, reaching backward to between the second coxae. Median border very prominent and divided by a median cleft into two lobes, the cleft extending below to the bases of the lateral lobes of mentum. Beside the cleft on either side is a single seta. The *lateral lobe* has a long and slender movable hook, near the base of which on the superior margin are three small setae. Terminal border with three dents, the middle one the largest, the upper one somewhat smaller with a few denticulations on its upper margin, end hook small, curved downward. Inner margin of lobe slightly convex and serrulated. End tooth of *maxilla* with three small basal teeth, followed below by 15 setae. Upper inner margin beset with three large equally sized teeth, of which the last one is more curved, followed below by about 9 setae. *Mandibles* two branched, the outer branch with five teeth of about equal size; right mandible with a basal tooth on the largest ventral dent; inner branch of right mandible with one tooth and a rounded prominence; that of the left mandible with a truncated and three-toothed plate. *Prothorax*: dorsum on each side with a toothed prominence, between this point and the median a brown band, widening to the middle in a half circular figure. Sides of prothorax black. Sides of *synthorax* for the most part dark brown to black, originally (in younger stages) separated into four bands, in the ult. instar these bands are confluent. *Wing-pads* reaching to the end of segm. four. *Legs* with the femur and tibia both marked with three dark cross bands; these markings are darkest in the fore legs and paler in the hind legs. End of tibia and

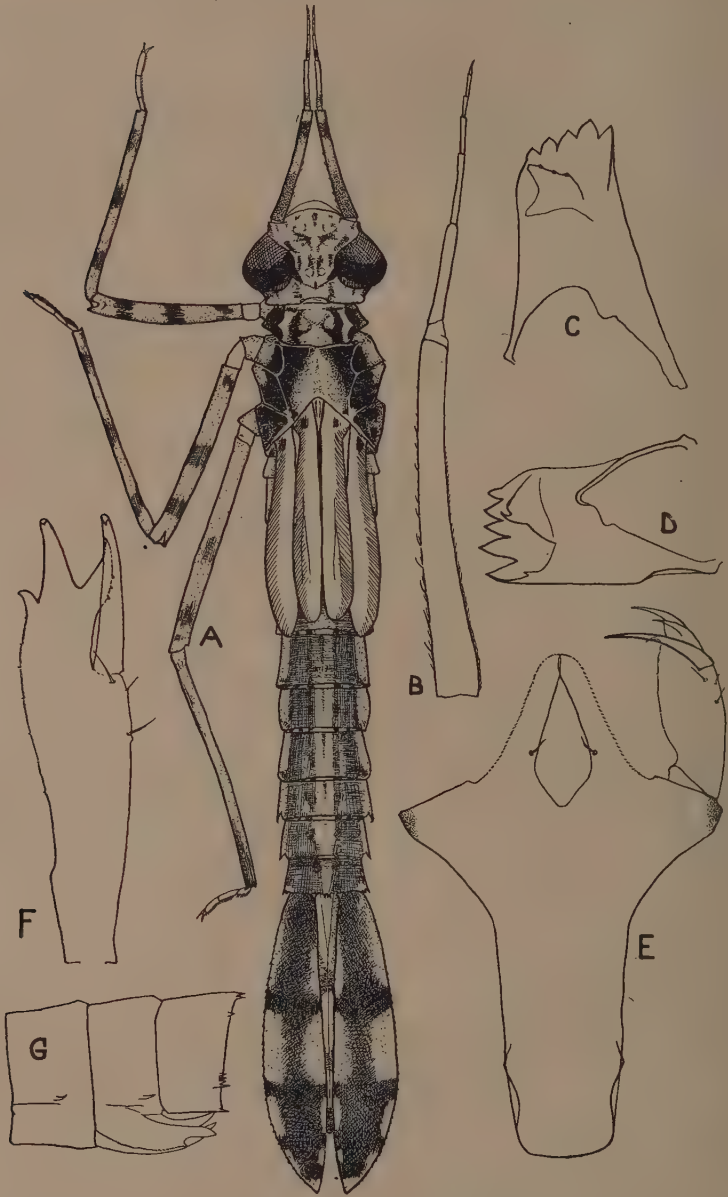


FIG. 1.—*Hetaerina macropus* Selys. A, dorsal view of full-grown female nymph; B, right antenna; C, left mandible, inner side; D, right mandible, inner side; E, mentum, inner side; F, right lateral lobe of mentum; G, end of abdomen of female, left lateral view.

first tarsal segment beset with plumose setae. *Abdomen* has on either side three darker longitudinal bands, with the result that the middle part and the flattened sides are pale. These three side bands are partly confluent. On each segment over the median is a fine black stripe not reaching the end of the segment. Along the median and at the end of the segments in the darker side bands are some darker spots. Segments 8 and 9 with lateral spines, segm. 10 with a few short spines on the lateral carina and with 3 such spines in the dorso-median on the hind margin and one spine on each side more ventrally. Underside of abdomen mostly darkened, lighter in the middle part, but marked with a fine black median line. *Gonapophyses* of female reaching to near the end margin of segm. 10, outer pair (valvae) with the ventral margin partly serrulated; end tooth large. End gills long, lateral gills triquetral, the outer margin slightly curved, the form lanceolate; length: width = 5.1, margins finely serrulated; the gills marked with 4 dark cross bands, the last one at the tip partly developed, base and middle part of the gill darkened, connecting the cross bands. The median gill flat and shorter than the laterals, marked with 3 darker cross bands. Total length, including first antennal joint and abdominal gills, 24 mm., first ant. segm. 2.7 mm., abd. 10 mm., lateral gills 7 mm., largest width of head 3 mm.

One ult. female nymph and several younger instars examined.

Nymphs of *Hetaerina macropus* were commonly met with in different stages in a creek on Orange Hill Road in Tobago. They very probably belong to this species, as imagines of it were abundant in that spot and because no other species of *Hetaerina* is found in the island of Tobago.

This nymph is best characterised by the lanceolate lateral abdominal gills, a lateral spine on abdominal segments 8-9, one seta along each side of the median mental cleft and by a row of not distinct small setae along the inner margin of the first antennal joint. It forms the seventh species of *Hetaerina* known in the nymphal stage, and to separate it from the other ones the following key may be of some help to the student.³

1. Abd. segm. 7-9 with lateral spines 2.
- Abd. segm. 8-9 with lateral spines 3.
2. Lateral abd. gills long, lanceolate, not dilated in the apical half, middle tooth on terminal border of lateral mental lobe much longer than the upper one *americana*.
- Lateral abd. gills dilated in the apical half, middle tooth on terminal border of lateral mental lobe equal in size to the upper one *moribunda*.
3. Abd. segm. 3-10 with an apical middorsal knob, 2 setae on each side of mental cleft sp. (?).
- Abd. segm. 3-10 without such a knob, one seta on each side of mental cleft 4.
4. Lateral abd. gills dilated in the apical half; first antennal joint with 5-6 long setae along the inner side *dominula titia* (?).
- Lateral abd. gills lanceolate, not dilated in the apical half; first antennal joint with a row of short not distinct setae along the inner side *macropus*.

Genus *Argia*.

Among the collected nymphs of this genus there were three different kinds represented. This corresponds with the observation that only three species of *Argia* were found in the island. To which species each belongs is not easy to determine.

Once a transferring specimen of *Argia translata* was collected by me in

³ The description of the nymph of *Hetaerina californica* by Hagen (1880, *C.R. Soc. ent. Belg.* 23 : 65) was not available for consultation.

Surinam, and the skin of this example shows no difference from the long-gilled *Argia*-nymph of Tobago, so that we may be quite sure about this species.⁴

The identification of the other two species is not so simple, as but one female specimen was full grown and suitable for an examination of the wing-venation. The venation in the wing-pads of this example was compared with the wing-venation of some female imagines of *A. difficilis* and *A. orichalcea*. It was found that there were no striking differences between this nymph and the imagines examined, but there seems to be rather more agreement with *difficilis* than with *orichalcea* in the number of postnodal cells to Rs and in the number of cells between Rs and M1a. For this reason the two species are doubtfully attributed to *difficilis* and *orichalcea*, until more complete material is at hand.

Argia translata Selys, fig. 2.

A moderately slender nymph with long gills and with a pale-coloured dark dotted body and legs. Among the species of *Argia*, hitherto described in the nymphal stage, it is the first type of a slender form resembling many Coenagrionids living in standing water.

Head broader than long (5:3), hind angles swollen and rounded, spinulose, a black stripe along the outer margin. *Antennae* thin and simple, 7-segmented, the first joint pale, otherwise brownish; relative length of the segments 13:19:37:24:15:9:6. *Mentum* broadly triangular, reaching backward to behind the first coxae, the sides diverging, armed with a row of small spines along the margin in the apical half; no mental setae present but basally there are on each side a few (4-5) small spines; median lobe moderately prominent (less than in *difficilis* and *insipida*), finely denticulated. Lateral lobe with one slender seta at base of movable hook and a small seta in the middle of the lobe; movable hook very long and curved, end hook much shorter than movable hook, but longer than terminal hook.

Maxilla of right side: end-tooth with two basal teeth, followed below by two rows of respectively 7 and 4 setae; inner side with three large teeth of equal size, followed below by 6 larger setae and 3 smaller ones more laterally. *Maxilla* of left side: end tooth with two basal teeth, followed by two rows of respectively 8 and 5 setae; inner margin with three large teeth of equal size, followed below by two rows of respectively 6 and 4 setae. *Mandibles* with five unequally-sized teeth, right mandible with a small tooth at base of the first large terminal tooth and with one blunt tooth inferiorly; left mandible inferiorly with two small blunt teeth; outside of both left and right mandible, with a transverse row of small setae and with some spines more basally. *Prothorax* with hind margin rounded. *Synthorax* broader than prothorax, dark brown with some paler spots at dorsum. *Wing-pads* in the second-ult. instar reaching to the end of abd. segm. 2. *Legs* relatively long, femora very little flattened, mostly pale but marked with black rings on both femora and tibiae, with two distinct rings and at base of femur and at the knee of tibia with a less conspicuous ring; apical end of tibiae with simple and divided (trident and plumose) setae, tarsi with plumose setae only. *Abdomen* slender, tapering to the end, dorsum with a broad pale stripe over the median, followed each side by three more or less confluent darker dotted bands; segment 7-10 somewhat spinulose. Male gonapophyses small, triangular, sharp pointed, ventrally with one row of 3-4 short spines, reaching backward to the apical fourth of segm. 10. Female gonapophyses (in second-ult. instar) extending backward to half-way segm. 10, ventral margin of outer pair with one row of 3-4 small spines. Ventral end margin of segm. 10 with a single row of equally-sized spines. *Gills* long, lanceolate,

⁴ The description of the nymph of *A. translata* by Garman (cited by Byers) is too incomplete to allow of any conclusion being drawn about the specimens from Tobago.

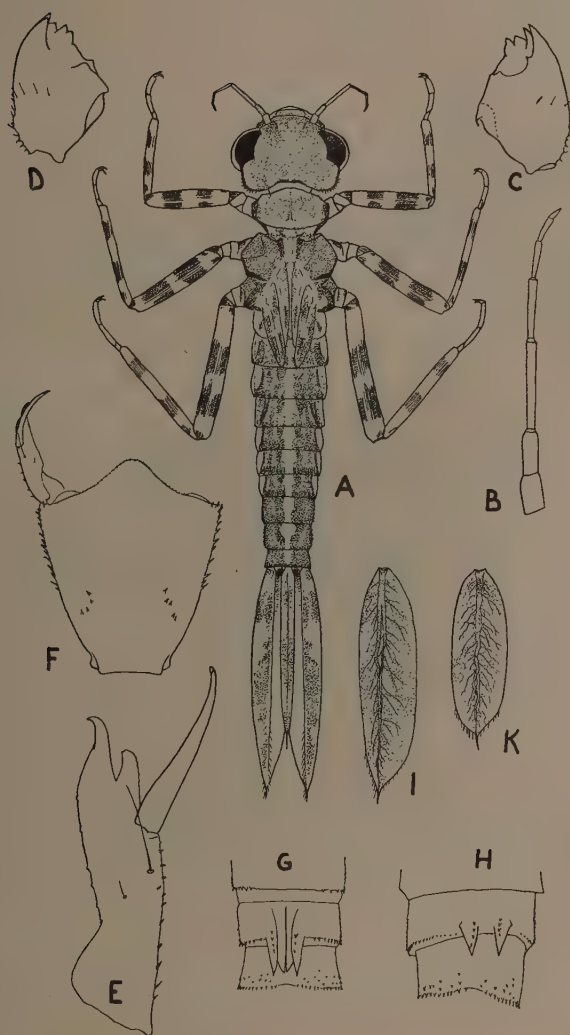


FIG. 2.—*Argia translata* Selys. A, dorsal view of second-ult. female nymph; B, right antenna; C, right mandible; D, left mandible; E, right lateral lobe of mentum; F, mentum, inner side; G, end of abdomen of female nymph, ventral view; H, end of abdomen of male nymph, ventral view; I, left lateral abdominal gill, left lateral view; K, middorsal abdominal gill, left lateral view.

with fine end point, the laterals longer than the middorsal gill, slightly pigmented with three cross bands. Gill veins conspicuous and branched in a simple way. Length of second-ult. female nymph: total, including gills, 16 mm.; gills 5 mm.; abdomen 6 mm.; width of head 3 mm.

Male exuvia: total length, including gills, 15.5 mm.; gills 5 mm.; abdomen 7 mm.; width of head 3.7 mm.

Tobago, Orange Hill Road Creek, 21st Oct. 1944 (Geijskes coll.). One exuvia and one second-ult. instar (♀) examined. There are still 4 younger stadia from this locality, probably belonging to the same species. The nymphs were found between roots floating in a small stream.

This type of nymph differs from the other known *Argia* nymphs by its slender body, the long lanceolate gills, the pale coloured and characteristic spotted body and the slender and pointed gonapophyses, armed with one row of small spines ventrally.

In its general appearance it resembles the common type of *Coenagrionid* nymphs living in standing water.

Argia "*difficilis*" Selys, fig. 3.

This is one of the stout-bodied stream-dwelling nymphs with a broad head and thorax and tapering abdomen, somewhat flattened legs and oval hypertrophied gills. The body is dotted with darker and paler spots and bands.

Head broader than long, hind angles swollen and rounded, spinulose, outer margin with black stripe. Antennae thin and simple, 7 segmented, first joint paler than the remaining segments, relative length of the segments is 16:21:35:24:12:8:5. *Mentum* broadly triangular, reaching backward to behind the first coxae, the sides diverging, armed with a row of small spines over the apical half; no mental setae present, but in the basal part each side with a row of 3 to 5 small spines; median lobe prominent and rounded, finely denticulated. Lateral mental lobe with one slender seta at base of movable hook, the latter long and curved, terminal hook slightly shorter than end hook, which is nearly as long as the movable hook. *Maxilla* of right side: end tooth with two basal teeth, followed below by 6 strong setae and several rows of finer setae, in total 16; inner side with three large teeth of equal size, followed below by 7 larger setae and 6 slender setae more laterally. *Maxilla* of left side: end tooth with two basal teeth, followed by two rows of, in total, 22 setae; inner margin with three large teeth of equal size, followed below and more laterally by about 12 setae. *Mandibles* with five unequally-sized teeth, right mandible with a small tooth at base of the first larger terminal tooth and with a blunt tooth more inferiorly; left mandible inferiorly with two small teeth; outer side of both left and right mandibles, with a transverse row of small setae and some spines more basally. *Prothorax* broader than long, sides dark brown, hind margin nearly straight. Synthorax large and broad but smaller than head; brown; the wing-pads in the female reaching to the middle of abd. segm. 6; in the male to the end of abd. segm. 4. *Legs* large, the femora flattened, for the most part pale, marked with black rings, two on the femora and three on the tibiae; apical end of tibiae with simple, divided (trident) and plumose setae, tarsi with plumose setae only. *Abdomen* relatively broad and stout, tapering to the end, each side with two dark brown bands, which are confluent in the apical half of dorsum, remaining in the median, a diffuse pale stripe. Segments 7-10 spinulose. Male gonapophyses broadly triangular, pointed, on each of them ventrally two rows of short spines, extending backward to the apical fourth of segm. 10; female gonapophyses: inner pair somewhat longer than outer pair, reaching to the end of segm. 10, ventral margin of the valves (outer pair) armed with two rows of small spines, but no spines on the end-tooth. Ventral end margin of segm. 10 with a single row of equally-sized spines. *Gills* swollen, oval lanceolate, with an end point, the

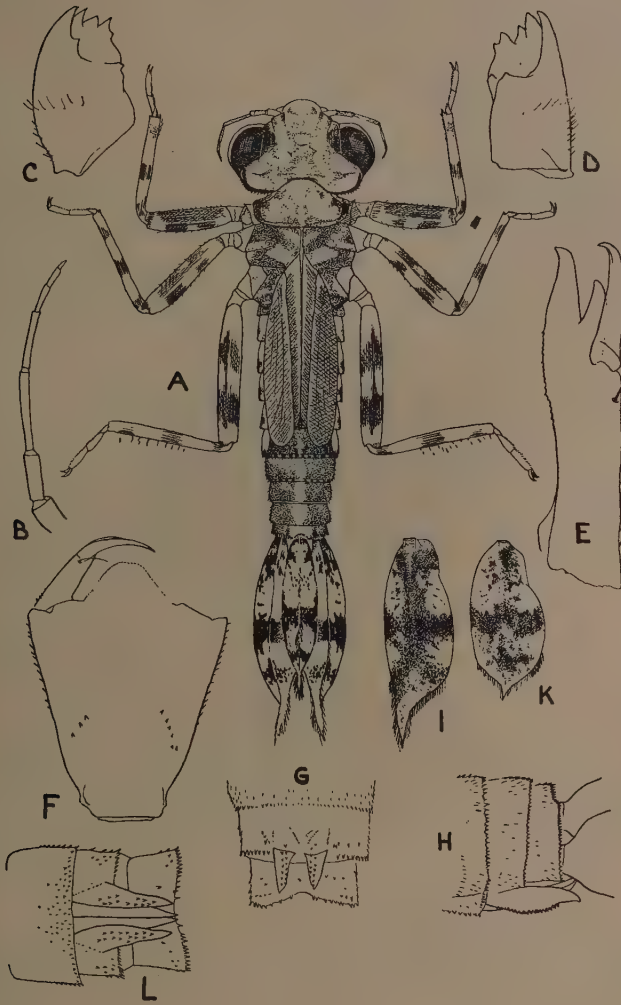


FIG. 3.—*Argia difficilis* Selys. A, dorsal view of full-grown female nymph; B, right antenna; C, right mandible; D, left mandible; E, right lateral lobe of mentum; F, mentum, inner side; G, end of abdomen of male nymph, ventral view; H, end of abdomen of female nymph, lateral view; I, left lateral abdominal gill, left lateral view; K, mid-dorsal abdominal gill, left lateral view; L, end of abdomen of female nymph, ventral view.

laterals longer than the middorsal gill; pigmentation limited to three cross bands, of which the middle one is the darkest, the first (basal) and the third (apical) band are confused and in the median of the gill-blade more or less connected with the broader middle cross band. Total length, including gills, 14.5-16 mm.; gills 4-5 mm.; abdomen 5-7 mm.; width of head 3.2-3.5 mm.

One male and one female ult. nymph examined from Orange Hill Road Creek.

Argia orichalcea Hagen, fig. 4.

Head broader than long (3 : 2), hind angles swollen, rounded and spinulose, with a black stripe from the eyes along the outer margin. Antenna simple and practically without hairs or spines, uniformly brownish coloured, the first joint the palest. Relative length of

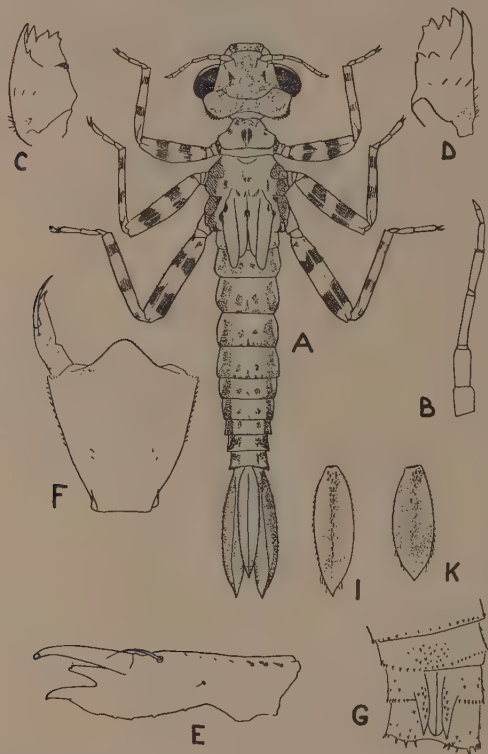


FIG. 4.—*Argia orichalcea* Hagen. A, dorsal view of a probable third-ult. female nymph; B, right antenna; C, right mandible; D, left mandible; E, right lateral lobe of mentum; F, mentum, inner side; G, end of abdomen, ventral view; I, left lateral abdominal gill, left lateral view; K, middorsal abdominal gill, left lateral view.

the segments : 13 : 16 : 24 : 17 : 11 : 7 : 4. *Mentum* broadly triangular, reaching backward to behind the first coxae, the sides diverging, armed in the apical half with a row of 11-12 short spines; no mental setae but in the basal part each side with two short spines; median lobe prominent, uncleft and the margin finely denticulate. Lateral lobe with one large

seta at the base of the movable hook and with a small seta more in the middle of the lobe; the upper margin with a row of 3 short and lanceolate spines and 4 smaller setae; movable hook long and curved, end hook shorter than movable hook but longer than the terminal hook. *Maxillae*, both right and left, on lacinia with one large end-tooth, followed by two shorter basal teeth and a fine sharp-pointed tooth at base of the second basal tooth, farther below a row of 8 setae and 4 setae laterally. Inner side with 3 equally-sized large teeth, followed below by a row of 4 setae and 3-4 smaller ones more laterally. *Mandibles* with five unequally-sized teeth, right mandible with a small basal tooth at the first large terminal tooth and with one blunt tooth inferiorly; left mandible inferiorly with two such blunt teeth; outer side of both left and right mandible with a transverse row of small setae and with some spines at base. *Prothorax* small and with a nearly straight hind margin, the side-lobes somewhat spinulose. *Synthorax* broader than prothorax, the sides dark brown, dorsum pale. Wing-pads in the third-ult. instar reaching to the apical fourth of abd. segm. 2. Legs with somewhat flattened femora, distinctly marked with two dark rings on the femora and tibiae and with a less conspicuous ring at base of femora and on the knees. Apical end of tibiae with divided (trident and plumose) and some simple setae, tarsi on the underside with plumose setae only. *Abdomen* slender, tapering to the end, dorsum with a broad pale stripe over the median; in this stripe on each segment 2 darker spots, which in the two last segments are confluent with a broad dark band on each side. *Female gonapophyses* with the outer pair furnished with short spines, more or less in two rows. Segm. 8 underside at base of the inner gonapophyses dotted with small spines. Outer ventral end margin of segm. 10 armed with several (5-6), somewhat curved strong spines. *Gills* moderately long, lanceolate and simple, the veins not visible; the laterals, in the basal half at the outer side, triangular, and flattened in the apical half. This margin beset with two or three rows of short spines. Colour grey without distinct bands or spots. Middorsal gill shorter, more rounded and with less short spines at the sides. Length of a probably third-ult. female nymph: total length, including gills, 12 mm.; gills (laterals) 3 mm., middorsal 2.6 mm.; abdomen 5 mm.; width of head 2.5 mm.

Tobago, Orange Hill Road Creek, 21st Oct. 1944 (Geijskes coll.).

Of this species only one specimen, unfortunately in a young stadium, was collected. It differs in many points from the foregoing species, so that it seems worthy of description. The points of difference are the following: the colour pattern of the abdomen, the form and structure of the gills and the large spines at the end margin of abdominal segment 10; the row of small spines at the mental lobe and the minute sharp-pointed third basal tooth on the maxillae.

Later on a re-examination of the full-grown nymphs in both sexes is to be undertaken.

The genus *Dythemis* (Hagen).

Of the 10 species known in the genus *Dythemis*, only three are described in the nymphal stage, viz. *velox* Hagen from Texas and *fugax* Hagen from Mexico, both by Needham (1904), and *rufinervis* Burmeister from Puerto Rico by Broughton Klots (1932). None of the nymphs of the continental South American species has been brought to light, although the genus is of neotropical origin, with offshoots to the north and south from Baja California, Texas and Florida to Argentine.

The nymph described below is referred to the genus *Dythemis*, on account of the following points in common with the other three described nymphs of this genus (cf. also the key to the genera in Needham and Fisher 1936):—

Eyes lateral in position and broadly rounded. Abdomen with spine-like middorsal hooks on segm. 3-9; lateral spines on abd. segm. 8 and 9; appendages, short triangular,

sharp-pointed, not curved downward. Crenulations of the distal margin of the lateral lobes of mentum, shallow; median lobe of the mentum prominent with a fringe of slender scattered spines (two on top). Legs long and thin. Tibiae and tarsus, except the 1st tarsus, with divided setae. Mandibles, according to the formula of Calvert (1927),

$$\begin{array}{l} \text{R } 1, 2, 3, 4, y, a, b, d \\ \text{L } 1, 2, 3, 4 \quad \quad a, b \end{array}$$

The obvious identification of this *Dythemis* nymph from Tobago is with *sterilis*, the only species of that genus known from Tobago. However, this is not a sure criterion; in Trinidad, beside *sterilis*, *multipunctata* Kirby and *cannacrioides* Calvert, are found, while the first is known also from Grenada and St. Vincent. As the nymphs of these species are not yet known, it is for the moment not possible to solve this question, so that it seems wise to refer the described nymphs of *Dythemis* from Tobago to *sterilis* only so long as no other data are at hand.

Dythemis sterilis Hagen, fig. 5.

One second-ult. instar and some younger stadia.

Head broader than long, the eyes broadly rounded and lateral in position, occiput rounded and spinulose. Antennae seven jointed, the segm. 3-6 with a black basal ring, relative length of the segments: 11, 13, 18, 16, 19, 22, 21. Mask triangular and covering the head ventrally for the most part, reaching backward to between the second coxae of the middle legs, sparsely spotted, but more densely spotted on the lateral lobes. *Mentum* broad triangular, with on each side inferiorly 9 setae, median lobe prominent with straight sides, these armed with 8 small but slender setae and with 2 such setae on top. *Labial lobe* with 8 long setae and a slender movable hook; the outer upper margin with a row of small spines to about half-way up the lobe, and, at base of the row of larger labial setae, a group of 6 finer setae. There are 9 obsolete crenulations on the distal margin of the lobe, each of them bearing 3 unequally-sized increasing downwards setae, or, with the large lower end hook included, 10 crenulations are present. *Maxillae* left and right side the same, showing on top of lacinia 7 unequally-sized, mostly strong and outward curved teeth; top of galea with one blunt tooth and a fringe of long setae. *Mandibles* on left and right side different. On both there is a row of 4 sharply-pointed but unequally-sized teeth at the distal margin. On the right mandible one small additional tooth is found at the lower inferior margin (y), whereas 3 black and blunt teeth are present in the inferior part (a, b, d); left mandible with no additional tooth at the lower margin and with two black and blunt teeth inferiorly.

According to Calvert the formula of the mandibles is $\begin{array}{l} \text{R } 1, 2, 3, 4, y, a, b, d \\ \text{L } 1, 2, 3, 4 \quad \quad a, b \end{array}$. *Prothorax*

and *synthorax* with a black to dark brown stripe along the sides, and with a more diffuse one over the middle of the dorsum, which is more or less separated and interrupted by a fine pale line in the median and widened spots at the margins of the segments. Hind margin of prothorax convex, rounded, the hind angles bristled. *Legs* long and slender, scarcely armed with long fine hairs and short spines. Femora marked with 3 dark rings, of which the first one in the basal third is the darkest, just as is the middle one on the first tibia. Tibiae also with three darker cross rings; those on the hind legs fading. Apical end of tibiae and underside of tarsus-joints furnished with trident setae. Claws long and slender, slightly curved downward. *Abdomen* broader than head and thorax, depressed, the ventral side of which when alive probably works more or less as a sucker (the figured specimen is not typical and stretched beyond its normal size by alcohol, especially in the basal segments). Dorsum with dorsal hooks on segm. 3-9, these hooks sharp-pointed and reaching over the base of the following segment, those of segm. 7, 8 and 9 with a row of fine bristles on the

outer margin, and with some long hairs on those of the 9th segment. Hind margin of segm. 9 dorsally strongly concave, enclosing the small tenth segment ring. *Appendages*

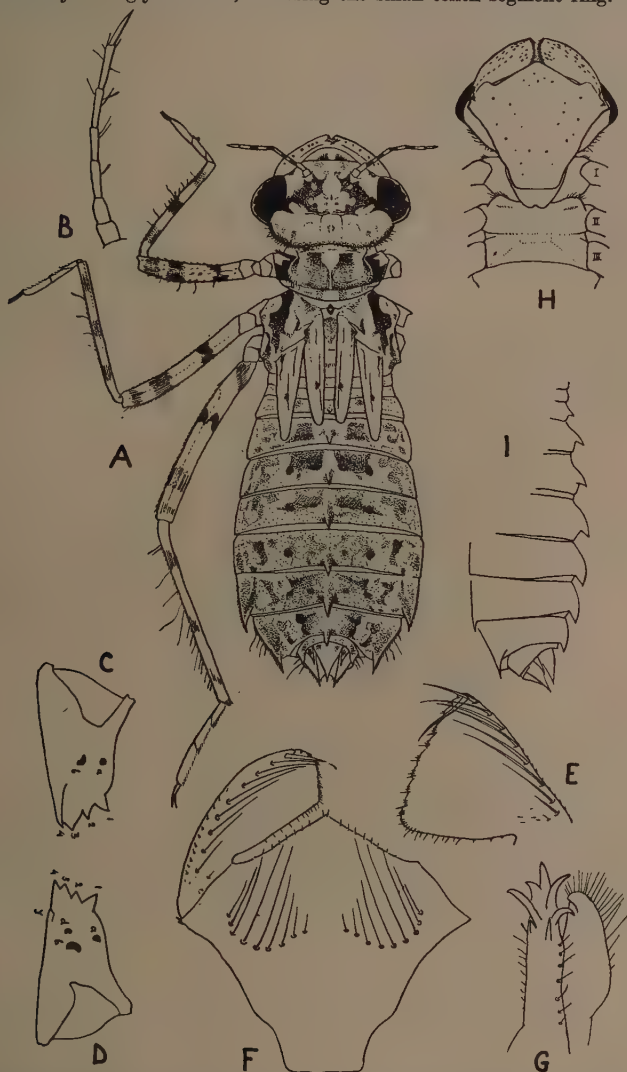


FIG. 5.—*Dythemis sterilis* Hagen. A, dorsal view of a probable second-ult. nymph; B, right antenna; C, left mandible, inner side; D, right mandible, inner side; E, right lateral lobe of mentum; F, mentum, inner side; G, right maxilla, top of lacinia and galea; H, head and thorax, ventral view; I, abdomen, left lateral view.

short-triangular, sharp-pointed, the inferiors hairy on the margin; the laterals about half as long as the dorsal appendage. Total length 12 mm.; width of head 3.5 mm., length of abdomen 7 mm.

This nymph is described from one, probably second-ult. instar, and some younger stages, all collected on the same spot in a creek on the Orange Hill Road in Tobago (21 Oct., 1944).

The following statement may be of some use to the student in distinguishing the described nymphs of *Dythemis*. The identifications are all provisional.

D. velox: mental setae 9-10, lateral setae 10; dorsal hooks on segm. 3-9 in a regular and even series, thin, flat, sharp-pointed, and that of the ninth segm. bent downward at tip; lateral spines on segm. 8 and 9, thin, flat, sharp, strongly convergent on 9.

D. fugax: mental setae (9-10)?, lateral setae (10)?; dorsal hooks on segm. 3-9 long, thin, sharp-pointed, reaching backward in the last three segments to nearly the base of the following hook; lateral spines on segm. 8 and 9, very thin and sharp, those on segm. 9 reaching backward nearly as far as the top of the appendices and four times as long as wide at base.

D. rufinervis: mental setae 10, lateral setae 7; dorsal hooks sharp and slender on segm. 3-9, decreasing in size posteriorly; small on 9; lateral spines on 8-9 short, on 9 slightly curved inward.

D. sterilis: mental setae 9, lateral setae 8; dorsal hooks on segm. 3-9 sharp and short, rounded and bent downward on segm. 7-9; lateral spines on segm. 8-9 stout, sharp-pointed.

9. LITERATURE CITED.

- ADAMSON, A. M., 1940, A second report on the Termites of Trinidad, B.W.I. *Trop. Agric.* **17**: 12-15.
- ALFORD, C. E. R., 1939, *The island of Tobago, B.W.I.* (Guide Book), Longmans, Dorchester, Dorset, England.
- BEARD, J. S., 1944, The natural vegetation of the island of Tobago, British West Indies. *Ecol. Monogr.* **14**: 135-63.
- BYERS, C. Fr., 1930, A contribution to the knowledge of Florida Odonata. *Univ. Fla. Publ. biol. Sci. Ser.* **1**, No. 1.
- CALVERT, P. P., 1901-1908, Odonata in: *Biologia Centrali-Americana*, Introduction and Supplement.
- , 1908, The Composition and Ecological Relations of the Odonate Fauna of Mexico and Central America. *Proc. Acad. nat. Sci. Philad.* **60**: 460-91.
- , 1927, Report on Odonata, including notes on some internal organs of the larvae. *Univ. Iowa Studies*, **12**, No. 2 (n.s. 132).
- DOWNS, W. G., GILLETTE, H. P. S., and SHANNON, R. C., 1943, A malaria survey of Trinidad and Tobago, B.W.I. *J. Nat. Malaria Soc.* **2**, Nr. 1 (Supplement).
- GEIJSKES, D. C., 1931, Notes on the Odonate-fauna of Trinidad, B.W.I. *Tijdschr. Entom.* **74**: xxxvii-xlii.
- , 1932, The Dragonfly-Fauna of Trinidad in the Br. W. Ind. (Odonata). *Zoöl. Meded.* **14**: 232-62; *idem* **15**: 96-128.
- , 1943, Notes on Odonata of Surinam IV. Nine new or little known Zygopterous Nymphs from the Inland Waters. *Ann. ent. Soc. Amer.* **36**: 165-84.
- KIRBY, W. F., 1894, On some small collections of Odonata (dragonflies) recently received from the West Indies. *Ann. Mag. nat. Hist.* (6) **45**: 261-9.
- KLOTS, E. Broughton, 1932, Odonata in: Scientific Survey of Porto Rico and the Virgin Islands. *Sci. Surv. P. Rico* **14**: 1-107.
- LAMONT, Norman, 1917, Note on the Butterflies of Tobago. *Agric. Soc. Trinidad and Tobago*, Publ. No. 701.
- NEEDHAM, J. G., 1903, Life Histories of Odonata Suborder Zygoptera. *Bull. N.Y. St. Mus.* **295**.
- , 1904, New dragonfly nymphs in the United States National Museum. *Proc. U.S. nat. Mus.* **27**: 685-720.

- NEEDHAM, J. G., & FISHER, E., 1936, The nymphs of North American Libelluline Dragonflies (Odonata). *Trans. Amer. ent. Soc.* **62** : 107-16.
- RIS, F., 1909-1916, Libellulinen : *Cat. Coll. Selys Longchamps*, Fasc. 9-16, 16^{2e}.
- , 1918, Libellen (Odonata) aus der Region der amerikanischen Kordilleren von Costarica bis Catamarca. *Arch. Naturgesch.* **82**, A, 9.
- WILLIAMSON, E. B., 1923, Some Peculiarities of the Dragonfly-Fauna of Trinidad (Odonata). *Ent. News* **34** : 263-5.

Vol. 97. Part 10. Pp. 237-252, 28 figs.

21st October, 1946.

THE
ST. ENT.
LIBRARY
101. 1048
Em. 344
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

	PAGE
X GARDNER, J. C. M. On larvae of the NOCTUIDAE (Lepidoptera)—II	237-252, 28 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 5s.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,
D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939.

Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

ON LARVAE OF THE NOCTUIDAE (LEPIDOPTERA)—II

By J. C. M. GARDNER, C.I.E., F.R.E.S.

(Forest Research Institute, Dehra Dun, U.P., India.)

Manuscript received 8th February, 1946.

(Read 5th June, 1946.)

WITH TWENTY-EIGHT TEXT FIGURES.

IN Part I of this paper (Gardner 1946) one of the groups discussed consisted of certain genera of the HYPENINAE (Group B II). Since that went to press Mr. Carl Heinrich has kindly given me an important paper, which I had not seen, on the classification of the larvae of that subfamily by S. E. Crumb (1934, *Ent. Amer.* 14: 133-97). Crumb pays far more attention to the setae of the head (and less to the structure of the mandibles) than I have done.

The present part deals with a number of genera, the larvae of which have certain significant structural characters in common, under the heading Division A; there are six subdivisions or Groups.

Division A.

The mature larvae of this division have the following combination of characters. The four ventral pairs of prolegs nearly equal in size (but the two anterior pairs distinctly smaller in *Callyna* Guenée). Seta III on A 8 is well above the spiracle and usually vertically above it (but slightly more anterior in *Borolia* Moore, *Stenopterygia* Hampson). Setal group VII is bisetose on A 1 and trisetose on A 2 (except when verrucae are present in group A 1).

The crochets are homoideous and uniordinal (except in group A IV). Body setae very short to long; secondary setae or verrucae present only in group A I. On T 2 and T 3 VI is unisetose (*Brithys* Hübner, with VI bisetose is omitted).

The division is subdivided on larval characters into groups as follows: A I (ACRONICTINAE with *Cetola* Walker (AMPHIPYRINAE)); A II (AMPHIPYRINAE, HADENINAE and part of EUXOINAE; A III (EUXOINAE, part)); A IV (MELICLEPTRINAE or HELIOTHINAE); A V (ACONTINAE, part) and A VI (AGARISTINAE, *Callyna* (AMPHIPYRINAE), *Tiracola* Moore (HADENINAE)) and *Churia* Moore of the ACONTINAE.

Although the position of seta III on A 8 with regard to the spiracle appears to be a useful and easily seen character it may not necessarily indicate natural relationship, for in two American species of AMPHIPYRINAE, namely *Achatodes zeae* Harris (Silver, 1933, *Tech. Bull. U.S. Dep. Agric.* 345) and *Papaipema nebrio* Guenée (Decker, 1931, *Iowa State Coll. Agric. Bull.* 143), seta III is described as being well cephalad to the spiracle; both species are borers in stems.

Key to Groups.

1. Secondaries present, at least six setae externally on ventral prolegs, or if fewer, pubescent gibbosities present on certain abdominal terga.
Body setae long (except *Cetola* with a mediodorsal stalked sphere on A 1). Often with verrucae A I.
- Without secondary setae; ventral prolegs with three external setae 2.

2. Adfrontal sutures extending to vertical sinus. (Body skin finely to coarsely granulate. Setae on distinct plates) A III.
- Adfrontal sutures meeting well before vertical sinus 3.
3. Crochets biordinal. (Skin closely covered with skin-points visible with a $\times 10$ lens) A IV.
- Crochets uniordinal 4.
4. Setal rings flush with skin. Setae short A II.
- At least setae II on A 8 on tubercles; sometimes the tubercles weak but the setae long 5.
5. Thorax moderately to strongly swollen (ovate to globose). Setae II on A 8 on abrupt basal projections (or together on one projection). Anterior body setae flush with the skin and short A V.
- Thorax not swollen. Setae II of A 8 on weak to strong tubercles. Some of anterior setae usually with basal tubercles (weak or absent in *Callyna*). Setae at least moderately long. A VI.

Group A I.

This group was discussed in Part I of this paper and consists mostly of ACRONICTINAE. The presence of secondary setae or verrucae does not by itself define the group since a few unallied species of NOCTUIDAE are known with secondaries.

Group A II.

Mature larvae.—Ventral prolegs nearly equal. Seta III vertically above the spiracle on A 8 (slightly more anterior in *Borolia*). Adfrontal sutures meeting well before vertical sinus. Without secondary setae. Setae always short; not at all raised basally. Group VI (above legs) unisetose on T 2 and T 3. Group VII bisetose on A I, trisetose on A II. Crochets uniordinal.

The larvae are smooth skinned; A 8 often tumid dorsally. Ocellus 1 usually very close to ocellus 2 but *Polytela* Guenée is an exception. Frontal setae usually nearly in line with frontal pores. Crochets uniordinal, simple.

Larvae included in Group A II belong mostly to genera classified as AMPHIPYRINAE and HADENINAE; in addition are *Agrotis c-nigrum* (EUXOINAE) which differs from Group A III in that the adfrons does not extend to the vertical sinus and *Lyncestis amphix* Cramer which seems to fit here although the adult comes under the NOCTUINAE.

Chasmina Walker, *Androlymnia* Hampson and *Elydna transversa* Walker, treated as AMPHIPYRINAE on adult characters, have been placed in group B I because of the very different larval structure (Gardner 1946).

Key to larvae of group A II.

1. Mandible with distal margin entire, at most with two minute angulations on the slightly produced middle part. (Spinneret at most moderately elongate, parallel sided, the apex with filamentous processes. Spiracle of A 8 twice or nearly twice as large as that of A 7) . . . (2).
- Distal teeth of mandible weak, the corresponding grooves on outer face distinct; there is no internal tooth. (Spinneret broad, the truncate apex with two fine approximate processes)
Spodoptera mauritia Boisduval.
- Mandible with sharply defined distal teeth (5).

2. Seta III of A 8 not quite vertically above the spiracle, slightly more anterior. Spiracle of A 7 very small, less than half A 8
Borolia byssina Swinhoe.
- Seta III of A 8 directly above spiracle. Spiracle of A 7 not quite so small (3).
3. Setal rings of body on very small shining plates. (Spiracles black)
Cirphis unipuncta Haworth.
- Setal rings not on such plates (4).
4. Labral emargination right angled. (A blackish line borders adfrons on each side and continues on each side of coronal suture to hind margin)
Polia consanguis Guenée.
- Labral emargination narrower. (Head without such black lines)
Sideridis yu Guenée.
5. Mandible with distinct internal tooth (6).
- Mandible without internal tooth (10).
6. Spinneret very long and slender. Labral emargination acute, a third deep.
(Internal tooth of mandible very small) *Stenopterygia subcurva* Walker.
- Spinneret short and wide. Labral emargination shallow (7).
7. Adfrons extending over nearly one-half of coronal suture which is slightly shorter than frons. Internal tooth of mandible smaller
Agrotis c-nigrum L.
- Adfrons including only a small part of coronal suture. Internal tooth of mandible larger (8).
8. Basal segment of labial palp scarcely longer than wide
Lyncestis amphix Cramer.
- Basal segment of labial palp elongate (9).
9. Spinneret strongly transverse, not fringed. Internal tooth of mandible with crenulate margin. Apical seta of labial palp very short, subequal to second
Perigea spp.
- Spinneret not strongly transverse, fringed distally. Internal tooth of mandible acute, not crenulate. Apical seta of labial palp much longer than second
Odontestra submarginalis Walker.
10. Spinneret not longer than wide, broad at apex. Ocellus 2 closer to 3 than to 1. (Body black with conspicuous red and white spots)
Polytela gloriosae Fabricius.
- Spinneret longer than wide. Ocellus 2 not closer to 3 than to 1 (11).
11. Setal group VI (above legs) on all thoracic segments are on small shining black plates. Basal segment of labial palp only slightly longer than wide
Calogramma festiva Donovan.
- Without such plates. Basal segment of labial palp at least 1.5 times as long as wide (12).
12. Labral emargination distinctly less than right angled, one-third or more deep (13).
- Labral emargination approximately right angled or obtuse, usually about one-fourth deep (15).
13. Labral emargination more than half deep
Trachea indistans Guenée.
- Labral emargination less than half deep (14).
14. Basal segment of labial palp about 3 times as long as wide and longer than distal seta. Spinneret with narrow distal lobe. Spiracles black
Eriopus placodoides Guenée.
- Basal segment of labial palp about twice as long as wide, much shorter than distal seta. Spinneret truncate distally. Spiracles pale with black rims
Dipterygia indica Moore.
15. Spinneret (fig. 20) with long fine median apical projection. (Apical seta of labial palp extremely short, about as long as second segment)
Elydna reclusa Walker.
- Spinneret otherwise (16).

16. Spinneret about four times as long as wide, slender. Apical seta of labial palp much shorter than basal segment (17).
 Spinneret about twice as long as wide. Apical seta of labial palp about as long as basal segment (18).
17. Frontal setae nearly level with frontal pores. Seta IV on A 5 above the level of the spiracle. Apical seta of labial palp extremely short, equal to second segment *Dadica lineosa* Moore.
 Frontal setae above level of pores. Seta IV not above spiracular level. Apical seta of labial palp distinctly longer than second segment.
 Colour green with small circular black spots on some segments
Sasunaga tenebrosa Moore.
18. Length about 25 mm. Width of head about 1.9 mm. *Laphygma exigua* Hübner.
 Length about 45 mm. Width of head about 3.0 mm. *Prodenia litura* Fabricius.

Spodoptera mauritia Boisduval.

Sevastopulo, 1939, *J. Bombay nat. Hist. Soc.* 40 : 687.—Gardner 1941 : 268.

Labral emargination a small abrupt notch. Mandible (fig. 1) with distal margin crenulate, the teeth very weak but the corresponding grooves on outer surface distinct. Maxillary palp with penultimate segment longer than wide. Labial palp with basal segment about twice as long as wide; apical seta slightly longer than second. Spinneret (fig. 14) nearly twice as long as wide, parallel sided, the apex with two acute approximate processes.

Borolia byssina Swinhoe.

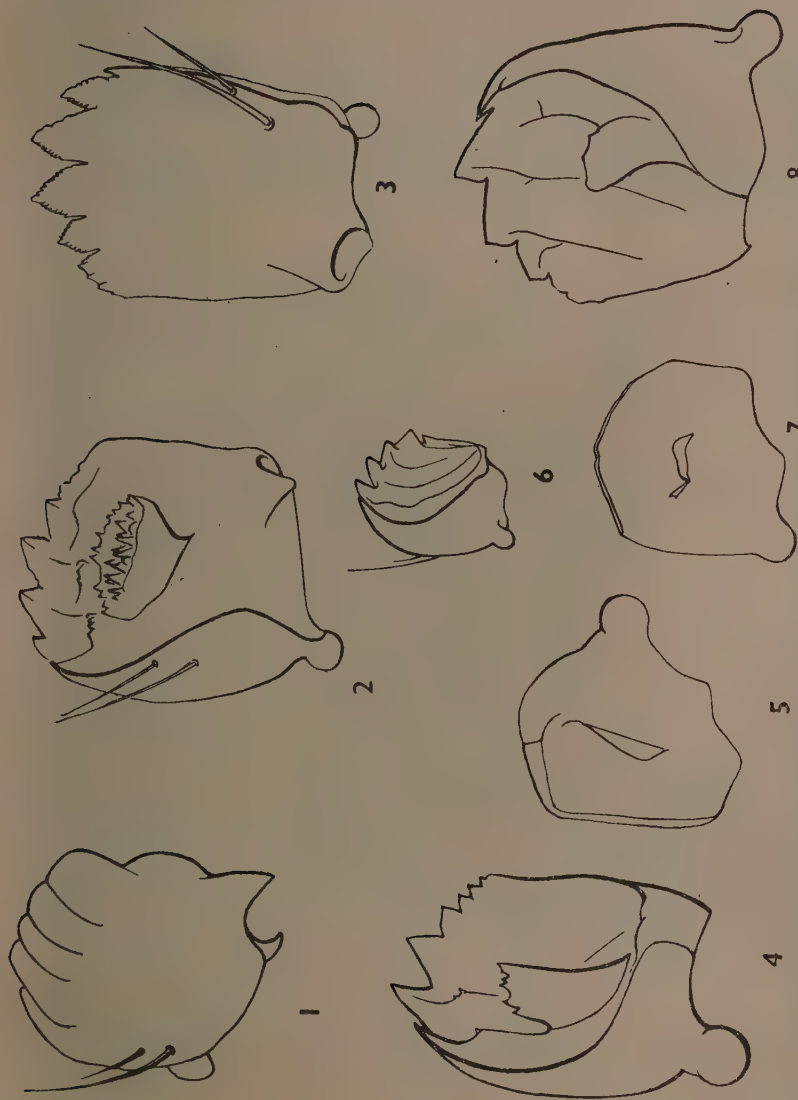
Frons much shorter than coronal suture. Labral emargination subacute, about one-third deep. Mandible (fig. 5) with distal margin entire; with a trace of an internal ridge. Maxillary palp with penultimate segment longer than wide. Labial palp with basal segment rather more than three times as long as wide; the distal seta slightly longer than second segment. Spinneret (fig. 12) nearly twice as long as wide, parallel sided, with several apical filaments. Seta III of A 8 well above spiracle but slightly more cephalad. Seta IV on A 4 to A 6 above spiracular level. Spiracle of A 7 slightly less than half that of A 8. Length about 30 mm.

Head sordid whitish, with dark reticulation and a dark line on each side of adfrons; frons with dark median line. Body closely mottled with dark brown; a distinct white spiracular line and vague dorsal pale lines; blackish paradorsal marks distinct in some specimens. Legs testaceous. Prolegs fuscous externally. Spiracles black. Larvae on grass; Dehra Dun, U.P.

Cirphis unipuncta Haworth.

Frons much shorter than coronal suture. Labral emargination subacute, nearly a third deep. Mandible with distal margin entire except for a feeble biangulation near middle; with a rather weak internal ridge. Maxillary palp with penultimate segment longer than wide. Labial palp with basal segment nearly three times as long as wide; apical seta nearly three times as long as second segment. Spinneret parallel sided, slightly longer than wide, fringed distally. Setal rings of body on small but fairly distinct shining plates. Spiracle of A 7 more than half that of A 8. Length about 35 mm.

Head sordid whitish with fine dark reticulation, a dark brown line on each side of coronal suture and adfrons; frons with dark median line. Pronotum dark brown with three white lines. Body above brown speckled with black; a broken irregular black line through seta II on each side; a vague white line through spiracles; below that pale with some reddish mottling. Legs pale. Prolegs fuscous externally. Setae on small fuscous pinnacula. Spiracles black. Larvae on *Zea mays* and grasses; Dehra Dun; Kulu.



FIGS. 1-8.—Mandibles, internal view except 1, 3. 1. *Spodoptera mauritia*. 2. *Calligya monoleuca*. 3. *Laphygma exiqua*. 4. *Perigea cupensis*. 5. *Borolia byssina*. 6. *Elydna reclusa*. 7. *Polia consanguis*. 8. *Odontestra submarginalis*.

Polia consanguis Guenée.

Frons much shorter than coronal suture. Labral emargination about a fourth deep, approximately right angled. Mandible (fig. 7) entire distally with feeble biangulation near middle; with weak irregular internal ridge. Maxillary palp with penultimate segment longer than wide. Labial palp with basal segment nearly three times as long as wide; apical seta short, about twice as long as second. Spinneret (fig. 22) about as long as wide, fringed at the wide apex. Spiracle of A 7 about half that of A 8. Length about 35 mm.

Head whitish with dark reticulation, a dark line on each side of coronal suture and adfrons; frons pale with dark median line. Body grey mottled with brown and some ill-defined black marks dorsally on posterior segments; without distinct pale stripes. Legs pale. Prolegs fuscous in part. Spiracles pale with black rim. Larvae on grasses; Dehra Dun and Garhwal.

Sideridis yu Guenée.

Sevastopulo, 1944, *J. Bombay nat. Hist. Soc.* 44 : 422.

Labral emargination abrupt, subacute, about a fourth deep. Mandible with transverse internal ridge, entire distally. Penultimate segment of maxillary palp longer than wide. Labial palp with basal segment three times as long as wide; apical seta short, about twice second. Spinneret nearly twice as long as wide, parallel sided, fringed at the apex. Spiracle of A 7 rather more than half that of A 8. Length about 25 mm.

Head olive brown. Body olive brown, minutely speckled with darker, with no longitudinal stripes except a pale subspiracular one distinct on thorax and disappearing on A 3. A dark spot above legs of T 2 and T 3. For further colour description see Sevastopulo. Preserved larvae were provided by Mr. Sevastopulo; Calcutta; from grasses.

Stenopterygia subcurva Walker.

Gardner 1941 : 270.

Labral emargination acute, a third deep. Mandible with small internal tooth and large distal teeth. Basal segment of labial palp nearly four times as long as wide, the apical seta three-fourths as long. Spinneret (fig. 21) slender, very long, about four times as long as basal segment of labial palp, rounded apically.

Agrotis c-nigrum L.

Crumb, 1929, *Tech. Bull. U.S. Dep. Agric.* 88 : 136 (ill.).

Head rather strongly transverse. Frons longer than the coronal suture, nearly half of which is included in adfrons. Labral emargination shallow and very obtuse. Mandible with distinct internal tooth which is smaller than the distal teeth. Labial palp nearly three times as long as wide; distal seta very short, scarcely longer than second. Spinneret (fig. 9) transverse, the wide apex with two filaments; with a postapical fringe. Spiracle of A 7 two-thirds that of A 8.

Head pale with some dark reticulation. Body pale yellowish-grey, speckled above with fuscous producing a more or less uniformly drab appearance, also with paradorsal black marks which become obscure on anterior segments; below a line through the spiracles the body is distinctly paler. Legs pale brown. Spiracles white with fine black rims. Length of body about 35 mm.

Described from larvae defoliating *Calendula* sp., Dehra Dun. This species, a widely spread agricultural pest, is described in detail by Crumb.

In 1941 I took larvae feeding on weeds in Kulu, Punjab, which superficially resemble this species; the reared adults also seem to be indistinguishable

superficially, although examination of the genitalia may show differences. These larvae, however, have an elongate tapering spinneret and a larger internal tooth to the mandible.

Lyncestis amphix Cramer.

Labral emargination a shallow curve. Mandible with large internal tooth and strong distal teeth. Basal segment of labial palp nearly as wide as long, the distal seta about as long. Spinneret (fig. 13) transverse, a median lobe distally with two minute points. Spiracle of A 7 about two-thirds that of A 8. Length about 40 mm.

Head pale brownish, with a transverse dark brown line posteriorly. Body pale green with white line on each side along the body. Spiracles with blackish rims, pale internally.

Larvae on *Cordia myxa* and *Ehretia laevis* (BORAGINACEAE); also recorded from *Ocimum sanctum*, *O. canum* (LABIATAE).

The adult is placed with the NOCTUINAE but the larva seems to be correctly placed in group A II. In the only mature larva I have seen VII is bisetose on the first but trisetose on the second abdominal segment.

Perigea spp.

Gardner 1941 : 269. (*P. capensis* Guenée, *Perigea* sp.)

Mandible (fig. 4) with sharp distal teeth; internal tooth large, its margin irregularly denticulate. Penultimate segment of maxillary palp slightly longer than wide. Labial palp with basal segment about three times as long as wide; apical seta slightly longer than second segment. The spinneret (fig. 15) very short, strongly transverse.

The *Perigea* sp. referred to in my previous paper has since been reared on *Ageratum conyzoides* and has been identified as *P. albomaculata* Moore.

Odontestra submarginalis Walker.

Frons subequal in length to coronal suture. Adfrontal sutures meeting well before middle of coronal suture. Labral emargination very shallow and obtuse. Mandible (fig. 8) with large triangular internal tooth; with three larger and one small distal teeth. Labial palp with basal segment nearly three times as long as wide; distal seta a little more than half as long as basal segment. Spinneret (fig. 10) scarcely longer than wide, the apex wide. Spiracle of A 7 about two-thirds that of A 8.

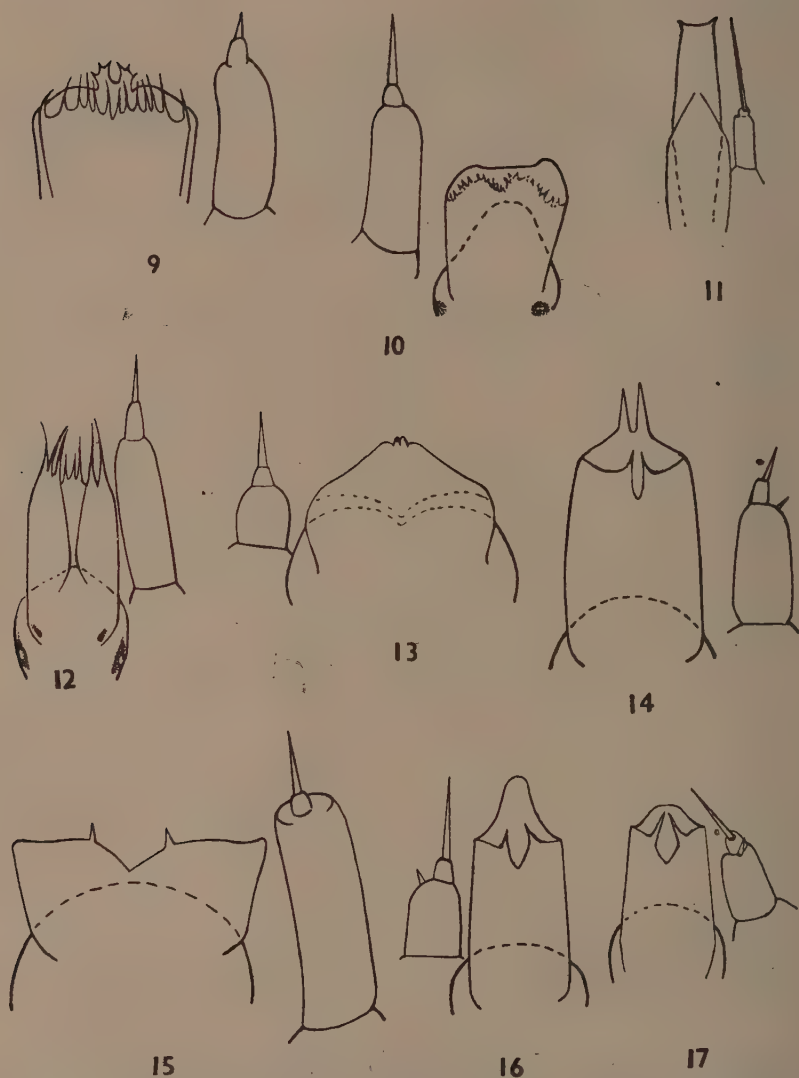
Head pale. Body speckled brownish-grey with a broad white line along the body below spiracles. Spiracles pale with black rims, set in blackish spots. Length about 35 mm. (Described from material in alcohol.)

Larvae were found in nursery beds containing seedlings of *Cryptomeria japonica*, Darjeeling (J.C.M.G. 1939).

Polytela gloriosae Fabricius.

Gardner 1941 : 267.

Ocellus 2 well separated from ocellus 1 and slightly nearer to ocellus 3 (in most related species ocellus 1 and 2 are closer). Spinneret (fig. 27) short and wide, somewhat wider distally, the apex sinuate, not fringed. Mandible without internal tooth; with four distal teeth, three of them large and acute. Labial palp with basal segment nearly three times as long as wide, the distal seta extremely short.



FIGS. 9-17.—Spinneret, and labial palp. 9. *Agrotis c-nigrum*. 10. *Odontestra submarginalis*. 11. *Dipterygia indica*. 12. *Borolia byssina*. 13. *Lyncestis amphix*. 14. *Spodoptera mauritia*. 15. *Perigea capensis*. 16. *Prodenia litura*. 17. *Laphygma exigua*.

Calogramma festiva Donovan.

Sevastopulo, 1939, *J. Bombay nat. Hist. Soc.* **41** : 79.

Frons a little longer than coronal suture. Adfrontal sutures meeting near the middle of coronal suture. Labral emargination very shallow and obtuse, with a minute abrupt notch medially. Mandible with no internal tooth, with sharp distal teeth, three of which are larger. Labial palp (fig. 26) with basal segment only slightly longer than wide; apical seta about as long as first segment. Spinneret (fig. 26) a little more than twice as long as wide, gradually tapering but more abruptly at the membranous apex. Setal group VI on the three thoracic segments on small slightly convex shining blackish plates. Spiracle of A 7 about three-fourths as large as that of A 8.

Head black, the adfrontal area brown. Pronotum black, divided by three pale lines. A mediadorsal yellow line along the body and another subspiracular; dorsolaterally on each side a white line and some finer, irregular white lines; black marks are conspicuous on A 1 (a large transverse dorsal patch), above each abdominal spiracle, a paradorsal pair on A 8 and on pygidium. Legs black; prolegs with a black external plate; venter purple; spiracles black (see Sevastopulo for fuller details of colour).

Described from larvae provided by Mr. Sevastopulo; feeds on LILIACEAE; Calcutta.

Trachea indistans Guenée.

Gardner 1941 : 269.

The labral emargination rather more than half deep, acute. Mandible with no internal tooth; with five larger sharp teeth and very small teeth or crenulations distally. Labial palp with basal segment about three times as long as wide, the distal seta rather shorter. Spinneret (fig. 23) about two and a half times as long as wide, nearly parallel sided, rounded at apex, basal shield extending more than half-way. Spiracles pale internally with black rims.

Eriopus placodoides Guenée.

Labral emargination more than one-third deep, distinctly less than a right angle. Mandible without internal tooth, the distal margin with three larger teeth and several very small teeth. Labial palp with basal segment about three times as long as wide, the distal seta rather shorter. Spinneret (fig. 19) about four times as long as wide; slightly tapering, more abruptly narrowed to a narrow apical lobe; basal shield extending more than half-way. Spiracles black, that of A 7 about half as large as that of A 8.

Head pale green with a few fuscous marks posteriorly. Body green, each segment T 2 to A 8 with a pair of paradorsal fuscous inclined lines; a white spiracular line along the body. Length about 25 mm. Larvae feeding on a weed in Garhwal (Balwant Singh).

Dipterygia indica Moore.

Head transverse. Frons higher than wide and subequal to coronal suture. Labral emargination rather less than half deep, acute. Mandible with no internal tooth, with strong distal teeth. Labial palp with basal segment about twice as long as wide, the distal seta distinctly longer. Spinneret (fig. 11) about four times as long as wide, slightly tapering, apex transverse; basal shield elongate. Setal rings of body black. Spiracle of A 7 about two-thirds as large as that of A 8.

Head sordid yellow with fuscous mottling. Body dull grey with vague whitish lines

mediodorsally and two laterally; two oblique whitish marks on A 8; pronotal plate brown; spiracles pale with black rims. Length about 25 mm.

Larvae defoliating *Callicarpa macrophylla*, Dehra Dun. Cocoon oval, of soil bound with silk.

Elydna reclusa Walker.

Labral emargination obtuse, about a fourth deep. Mandible (fig. 6) with no internal tooth, with four strong distal teeth. Labial palp with basal segment about twice as long as wide, the distal seta extremely short, about as long as second segment. Spinneret (fig. 20) moderately long, gently tapering with fine acute median apical extension. Spiracle of A 7 three-fifths as large as that of A 8.

Head testaceous, darker anteriorly. Body dull drab with black dorsolateral marks which are more distinct on posterior segments. Spiracles black. Length about 20 mm.

Described from preserved larva provided by the Entomologist, Tea Research Institute, Ceylon. The larvae were feeding on decaying tea leaves.

The larva of *Elydna transversa* Walker, if my adults are correctly identified, is very different and I have discussed it under another group (B I).

Sasunaga tenebrosa Moore.

Frons higher than wide, about equal to coronal suture. Frontal setae well above the level of the frontal pores (not nearly in the same line as is usual in this group). Labral emargination about one-third deep, nearly right angled, broadly rounded at base. Mandible without internal tooth, with distinct rather short distal teeth and several crenulations. Labial palp with basal segment a little more than twice as long as wide, the distal seta very short. Spinneret (fig. 25) nearly four times as long as basal segment of labial palp, nearly parallel sided, apex of spinneret slightly expanded with numerous filaments, basal shield extending over more than basal half, acute apically. Spiracle A 8 nearly twice as large as that of A 7.

Head polished, greenish testaceous with black spots, two on the frons, and three on each side. Body green with the setae of the prothorax, setae I of A 1, setae I and II of A 8 and setae of pygidium on black spots; some of the lateral setae on small black spots. Spiracles black, that of A 8 in a red triangular spot. Legs black; prolegs with black external plate. Length about 35 mm.

Larvae on leaves of *Ventilago calyculata*, Dehra Dun. Cocoon ovate, of soil bound with silk.

Dadica lineosa Moore.

Labral emargination approximately right angled, about a fourth deep. Mandible with no internal tooth, with sharp distal teeth. Labial palp with basal segment nearly three times as long as wide, the distal seta very short, about as long as second segment. Spinneret (fig. 24) elongate, about four times as long as width near base, tapering, rounded apically. Seta IV on A 5, A 6 above the level of the spiracle. Spiracles of first seven segments very small, of A 8 twice that of A 7. Length about 30 mm.

Head testaceous red, dark brown anteriorly on each side of frons, which is pale with a median dark patch. Body dull drab with some vague pale lines, a black lateral spot on each side of T 2, T 3. Legs black, prolegs black externally. Spiracles black. Larvae feeding on an unidentified weed, Dehra Dun.

Prodenia litura Fabricius.

Gardner 1941 : 268.

Frons slightly wider than high, longer than coronal suture. Mandible with four distinct distal teeth and no internal tooth. Labral emargination rather more than a fourth deep, approximately right angled. Labial palp with basal segment nearly twice as long as wide, the apical seta slightly longer. Spinneret (fig. 16) about 2.5 times as long as wide, subparallel, with narrowed, rounded apical lobe. Length about 45 mm. Width of head 3.0 mm. The body usually with two black more or less triangular paradorsal marks on segments behind pronotum.

Laphygma exigua Hübner.

Lefroy, 1906, *Agric. J. India* 1 : 338, figs. 2-9.

The mature larva of this species is structurally very like that of *Prodenia litura* F. although considerably smaller (length about 25 mm.; width of head about 1.9 mm.). The mandible, with sharp distal teeth and no internal tooth, is shown in fig. 3 and the spinneret in fig. 17.

Lefroy notes that the colour is very variable, from dark to mostly green. In four larvae sent me by Mr. P. J. Deoras the head (including frons) is mostly blackish, the body with a fine pale line on each side paradorsally; a blackish mark bordered externally by the pale line, on each segment; below each pale line is a dark band; a subspiracular pale band; spiracles with fine black rim and pale interior. In four larvae found on lucerne in Dehra Dun the colour is lighter, the head with dark brown reticulation, the body with no paradorsal series of black marks.

Group A III.

The species in this group belong to the EUXOINAE. To my previous summary of larval characters (Gardner 1941 : 266) may be added: Mandible without internal tooth, with strong distal teeth; spinneret short and broad, usually notched apically.

Agrotis ypsilon Rottemburg has been described in great detail by Crumb (1929 : 52); I have taken larvae feeding on weeds in Kulu, Punjab. The skin with well-separated, coarse and slightly convex granulation and with much finer interspersed granules.

Euxoa spinifera Hübner also with rather coarse granules but these are much more convex, subconical.

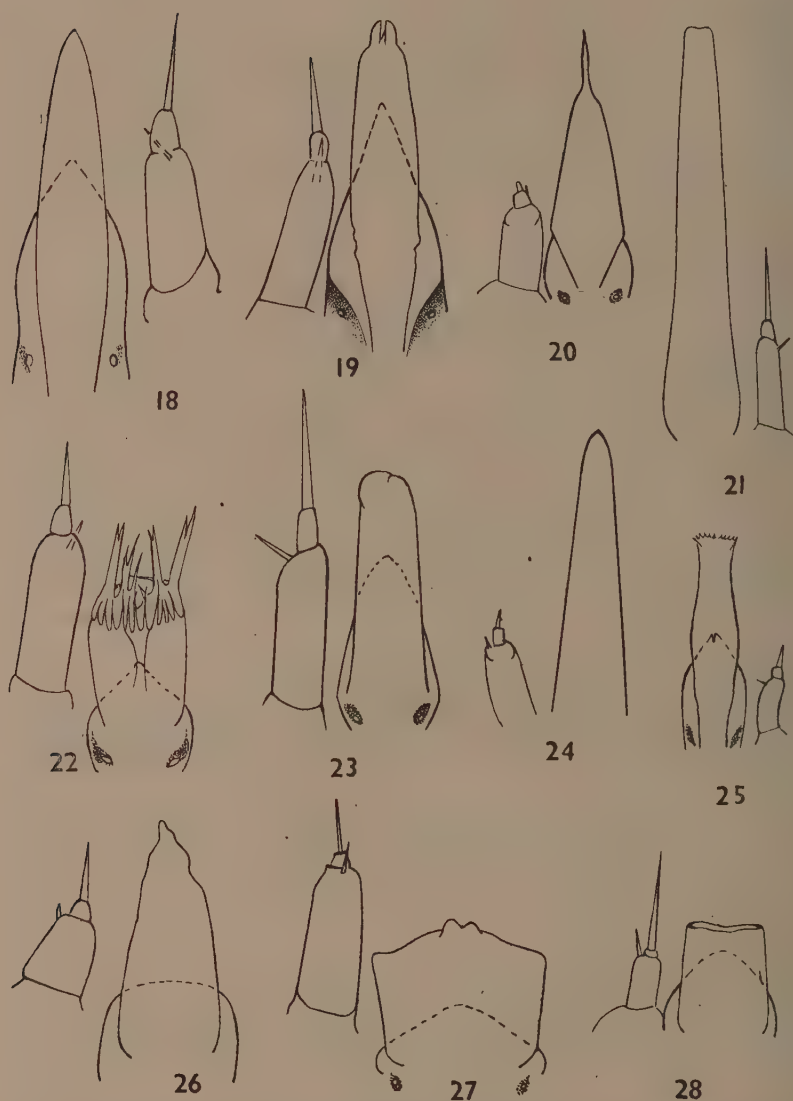
Euxoa intracta Walker, on weeds and grass in Dehra Dun, resembles *E. segetis* Schiffermüller (Gardner 1941 : 266) in the skin being extremely finely and closely granulate.

Agrotis c-nigrum L. is treated under Group A II, since the adfrons does not extend to the vertical sinus and the mandible has an internal tooth.

Group A IV.

This group was discussed in Part I of this paper and contains *Heliothis* Hübner, *Adisura* Moore and *Pyrrhia* Hübner. In Heslop's *Check-List of British Lepidoptera*, 1945, *Pyrrhia* comes with *Heliothis* in the subfamily HELIOTHINAE and this arrangement is in accordance with the structure of the larva.

I had overlooked an important paper by Crumb (1926, *Proc. U.S. nat. Mus.*



FIGS. 18-28.—Spinneret and labial palp. 18. *Callyna monoleuca*. 19. *Eriopus placodoides*. 20. *Elydna reclusa*. 21. *Stenopterygia subcurva*. 22. *Polia consanguis*. 23. *Trachea indistans*. 24. *Dadica lineosa*. 25. *Sasunaga tenebrosa*. 26. *Calogramma festiva*. 27. *Polytela gloriosae*. 28. *Aegocera venulia*.

68, art. 16) on larvae of *Heliothis*. In his diagnosis of generic characters Crumb points out that the prespiracular setae (IV, V) of T 1 are in a horizontal line: they are so also in *Adisura* but in a slightly oblique line in *Pyrrhia*. He also mentions that the apical seta of labial palp is short: it is much shorter than the basal segment in the three genera I have seen. Crumb does not mention biordinal characters.

Group A V.

Mature Larvae.—Prolegs normal, the four ventral pairs nearly equal; crochets unioordinal. Seta III on A 8 is vertically above the spiracle. Setal group VII is bisetose on A I and trisetose on A II. There are no secondary setae. All setae short. Thorax strongly to moderately swollen. All body setae flush with the skin except setae II on A 8, which are borne on abrupt conical protuberances (or together on one mediodorsal protuberance). Frons distinctly shorter than coronal suture. Junction of adfrontal sutures distant from vertical sinus. Pupation in silken cocoons on leaves or bark.

The mandible with distal margin having two weak teeth near the middle. Body skin smooth (minutely granulate in part under high power). Spinneret distinctly longer than wide but not reaching much beyond apical seta of labial palp.

This group of larvae contains four genera (*Aiteta* Walker, *Carea* Walker, *Maurilia* Moeschler, *Pseudelydna* Hampson) which are included in the ACONTINAE of Hampson (1912, Phalaenae).

Key to species.

1. Setae II of A 8 borne together on a mediodorsal projection. (Thorax globose) *Carea subtilis* Walker.
- Setae II of A 8 on separate tubercles. 2.
2. Thorax strongly swollen. Labral emargination nearly half deep. . . . 3.
- Thorax only moderately enlarged. Labral emargination less deep *Maurilia iconica* Walker.
3. Head distinctly granulate 4.
- Head smooth *Pseudelydna rufostava* Walker.
4. Paradorsal tubercles on A 8 more prominent, rather longer than wide *Aiteta truncata* Walker.
- Tubercles on A 8 short and stout *Aiteta apriformis* Walker.

Aiteta truncata Walker defoliates *Terminalia tomentosa* in Coorg. The other species in the key were previously briefly described (Gardner, 1941); the *Aiteta* sp. of that paper (page 278) has since been identified as *A. apriformis* Walker.

Group A VI.

Mature larvae.—Prolegs normal (but in *Callyna* the two anterior pairs rather markedly reduced). Seta III on A 8 is vertically above the spiracle. Setal group VII is bisetose on A 1 and trisetose on A 2.

Setae II of A 8 each on a weak to strong tubercle; where these tubercles are weak the body setae are long. Some of the other dorsal setae also usually on tubercles.

Junction of adfrontal sutures distant from vertical sinus. Crochets homoideous, unioordinal. Body setae moderate to long; secondaries absent. Pupation in the earth except *Churia* which makes fusiform cocoons on twigs.

Included here are *Callyna* (AMPHIPYRINAE), *Tiracola* (HADENINAE), *Churia* (ACONTINAE), *Aegocera* Latreille, *Eusemia* Dalman (AGARISTINAE).

Key to species.

1. A 1 with setae II each at the apex of a projection which is distinctly longer than wide; seta III on a similar but rather smaller projection; setae I on this segment on very small tubercles . . . *Churia nigrisigna* Moore.
 Setae II of A 1 at most on small tubercles which are not larger than those bearing setae I 2.
2. A 1 with setae I borne on abrupt projections; setae II on minute tubercles. (Spinneret short, broad, parallel sided and truncate apically)
Tiracola plagiata Walker.
 If setae I on A 1 are on tubercles, these small and not much stronger than those of setae II 3.
3. Spinneret slender, pointed apically. Anterior two pairs of prolegs distinctly smaller. Body setae moderate *Callyna* spp.
 Spinneret short and wide, not narrowed at the truncate apex. Prolegs nearly equal. Setae long 4.
4. Tubercles of setae I and II on A 8 abruptly raised. Labral emargination abrupt. Head and legs black *Eusemia adulatrix* Koll.
 Tubercles on A 8 very weak. Labral emargination very shallow. Head and legs mostly reddish *Aegocera venulia* Cramer.

Churia nigrisigna Moore was previously described (Gardner 1941 : 281).

The spinneret is long and slender with fine apex. Labial palp with elongate basal segment and long distal seta. Mandible with three sharp distal teeth. Body skin microscopically granulate. Feeds on leaves of *Grewia laevigata*.

Tiracola plagiata Walker.

Labral emargination a rather wide curve. Mandible sharply dentate apically; with internal tooth. Spinneret hardly longer than wide, broad, truncate apically. Setae moderately long, some of them on small tubercles but setae I of A 1 and II of A 8 on stronger, abruptly raised tubercles. In preserved specimens the head testaceous, castaneous anteriorly; body brownish with fine black strigulation; a pale irregular band below spiracles A 1 to A 3 and another below spiracles A 7 to A 8; a bracket-shaped black mark above on A 5, A 6. Spiracles pale with fine black rim. Length about 35 mm.

I am indebted to Mr. D. G. Sevastopulo for two preserved larvae taken by him in Darjeeling.

Callyna.

Generic characters.—Mandible (fig. 2) with sharp distal teeth and large internal tooth, which may be denticulate. Labral emargination widely curved at base. Spinneret (fig. 18) about twice as long as elongate basal segment of labial palp, slender, tapering to a point. Apical seta of labial palp nearly as long as basal segment. The two anterior pairs of prolegs more noticeably reduced than usual in this Group. Setiferous tubercles II of A 8 abrupt, rather broadly conical; anterior tubercles of body usually reduced. Setae moderate. Larvae feed on leaves of BORAGINACEAE (*Cordia*, *Ehretia*); cocoons of tough woven silk and soil.

C. monoleuca Walker.

Internal tooth of mandible denticulate (fig. 2). Spinneret as in fig. 18. Labral emargination nearly one-third deep. Spiracles pale (white to ochreous) with fine dark rims (in the other species the spiracles are black). The general colour is variable, the head pale or dark testaceous (without black spots), the frons white; the body may be pale green with

yellow lines along the body, one dorsomedian and three on each side, and with black marks dorsally on A 2; or there may be a strong development of black as transverse bands on the dorsum, a dorsolateral line on each side and a broken irregular band ventrolaterally, the intervening spaces yellow to whitish; blackish patches between prolegs; legs reddish to blackish, prolegs reddish to testaceous. However, before entering the soil for pupation and without moulting, the colour becomes generally dark closely mottled with dark brown, a median white spot on A 2 and the head develops a large brown anterior patch. Larvae feed on leaves of *Cordia myxa* and *C. macleodii*; Dehra Dun; Coorg.

C. jugaria Walker.

Structure very much as in *monoleuca*. Spiracles black. Head and pronotum testaceous red with black spots. Body pale bluish-white above with black marks having a tendency to form broken transverse lines; laterally ochreous speckled with black; legs black; prolegs testaceous with thick black concave mark at base. Before pupating the larva becomes dark brown, the black marks still visible, especially those bearing dorsal setae. Larvae on *Cordia myxa*; Dehra Dun.

C. contracta Warren.

Labral emargination rather less than a third deep, enclosing approximately a right angle (rounded at base). Mandible with internal tooth crenulate but not denticulate. Spiracles black. Head yellow with brown mottling and black spots. Body blue above and below, with a chrome lateral band on each side; dorsum with transverse thick and fine black lines; venter with much irregular black markings; legs black; prolegs yellow with thick black curved mark. Larvae on *Ehretia laevis*; Dehra Dun.

C. siderea Guenée (?).

Labral emargination more abrupt than in the other species, the sides nearly parallel, widely curved at base. Internal tooth of mandible with even margin. The smaller setiferous tubercles more distinct than in other species. Head testaceous with large black spots. Spiracles black. Body black with large ovate pale (? white) spots arranged in a dorsolateral series (mostly in pairs separated by a narrow black intersegmental line) and a similar series ventrolaterally; most segments with a small dorsal pale spot near centre; a few other small spots; A 8 pale above, the tubercles black; legs black; prolegs testaceous.

One larva from *Cordia myxa* Coorg is probably *C. siderea*, since that species was reared the previous year from the same plant and locality.

Aegocera venulia Cramer was previously described (Gardner 1941 : 294).

The labral emargination very shallow. Mandible sharply dentate distally, without internal tooth. First segment of labial palp less than twice as long as wide and shorter than distal seta. Spinneret (fig. 28) scarcely longer than wide, nearly parallel sided, truncate apically. Setiferous tubercles of body very weak. Feeds on *Boerhavia diffusa*.

Eusemia adulatrix Koll.

Labral emargination much more abrupt than in *Aegocera*. Mandible without distinct internal tooth. Spinneret much as in *Aegocera*. Setiferous tubercles rather stronger than in *Aegocera*; setae long. Head and legs polished black. Body with a reddish tinge but with six black lines along each side above level of prolegs, which are blackish. Pronotum black with a little reddish. Setae white, the tubercles black and set in black spots. Spiracles black. Length about 50 mm. Feeds on *Dioscorea belophylla*; Dehra Dun.

The larvae of two Indian AGARISTINAE are figured in colour by Moore (1858, *Cat. Lep. East India Co.*, plate 13). *Mimeusemia basalis* Walker (fig. 3) has a reddish head with black spots, the body yellow with black marks and long setae. *Zalissa transiens* Walker (fig. 5) from Darjeeling is shown as black, except T 1 and A 8 mostly yellow with black spots; setae long. Hampson (1894, *Fauna Brit. India Moths* 2: 148, 155) reproduces Moore's figure (but not in colour) and refers to lateral tufts of blue hairs, which, however, are not clear in my copy of Moore.

REFERENCES.

- CRUMB, S. E., 1929, *Tech. Bull. U.S. Dep. Agric.* 88.
GARDNER, J. C. M., 1941, *Indian For. Rec.* 6 (8).
—— 1946, *Trans. R. ent. Soc. Lond.* 96: 61–72.

Vol. 97. Part 11. Pp. 253-298, 11 figs.

30th October, 1946.

THE
TRANSACTIONS
OF THE
Eu. 344
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

X RICHARDS, O. W., M.A., D.Sc., and WALOFF, N. F.D.

The study of a population of *Ephestia elutella*

Hübner (Lep., PHYCITIDAE) living on bulk grain . 253-298, 11 figs.

PAGE

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 14s.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

THE STUDY OF A POPULATION OF *EPHESTIA ELUTELLA* HÜBNER (LEP., PHYCITIDAE) LIVING ON BULK GRAIN

By O. W. RICHARDS, M.A., D.Sc., and Miss N. WALOFF, Ph.D.

Manuscript received 24th September, 1945.

(Read 5th June, 1946.)

WITH 11 TEXT-FIGURES.

CONTENTS.

	PAGE
Introduction	253
2. The environment	254
3. Life-history of the moth in the warehouse	256
4. Estimation of numbers of adults	257
5. Estimation of numbers of eggs	263
6. Estimation of numbers of larvae	267
7. Parasites and predators	276
8. Second generation of moths	277
9. Diapause in fully fed larvae	278
10. Effects of crowding	283
11. Discussion of results	286
12. Acknowledgements	289
13. Summary	289
14. References	290
Appendix 1. Length of life of moths	291
" 2. The accumulated total of moths in 1943, and average weekly number in 1944	293
" 3. Fecundity of moths in 1944, and related topics	295
" 4. Observations in 1945	297

In the autumn of 1941 *Ephestia elutella* first became a serious pest of bulk wheat stored in a London warehouse. In 1941-42 preliminary observations were made on the infestation, and the possibility of investigating it quantitatively was examined. The present work, begun in 1943, aimed at devising methods of estimating the numbers of each stage of *Ephestia* throughout the season; also to endeavour to check each estimation in two more or less independent ways.

As the growth of the population is a continuous process, it was thought that each estimate would be checked by the succeeding one, e.g. larval numbers should be related to egg-numbers, etc. The sample areas on which counts were made were not arranged strictly at random but were chosen so that areas of different light intensity were well represented, but with this restriction the scheme was effectively random, particularly in 1944 when the same areas were used as in 1943, though the grain was differently placed in the room. Besides providing estimates of numbers, it was also hoped that the work would reveal some of the reasons for the changes in the size of the population. Studies of the behaviour of *Ephestia* (*Trans. R. ent. Soc. Lond.* 97) were made to help in devising sampling methods and to explain the observed distribution of moths and larvae.

2. THE ENVIRONMENT.

Early in 1943, by arrangement with the Ministry of Food, one room containing 500 tons of Manitoba wheat¹ was set aside for study. In February 1944, this lot of wheat was removed (the larvae all hibernating in the crevices of the room) and new wheat was brought in early in April 1944. This consisted of two lots, 197.3 tons of No. 1 and 322.1 tons of No. 2 N. Manitoba, separated by a bulkhead and a few feet of empty floor space.

The room was $100 \times 50 \times 8$ ft. and the grain lay on the floor, filling it to a depth 3-8 ft.; it was possible to crawl to almost any part. The grain was fed into the room from four rows of nine pipes about 1 ft. diameter and it tended to form cones near the pipes, with valleys between them. There was usually most free space along the walls (4-5 feet). The ceiling was supported by four rows of two large parallel beams supported on four rows of eight pillars. The positions of the pillars and pipes made it easy to map the room. The room had three windows at each 50-ft. end, and three along one 100-ft. side; these last three opened into an enclosed space ("the garner").

Though the floor space was 5000 square ft. the surface of the grain was greater. This was measured by taking several transects along which the distance of the surface of the grain from the ceiling was measured. From this a scale drawing was constructed and the average excess of the linear dimensions of the grain surface was estimated. The grain surface was 5-10% greater than the floor-space. The same measurements also gave an estimate of the average depth of the grain (*i.e.* by subtracting from the known height of the room). The averages were computed from 40 measurements scattered over the room.

The windows do not let in much light and the cones of grain shade the whole central area. Light measurements were made with a Holophane Lumeter kindly lent by Dr. W. D. Wright of the Dept. of Physics, Imperial College of Science and Technology. In front of windows, readings ranged from 1 to 10 F.C., but in most of the room the intensity was below 0.09 F.C. (a light at which reading is just possible) with considerable areas below 0.009. The light was always measured as reflected from the grain, walls, or ceilings but it made very little difference if the reflection from the white plate provided with the instrument was used instead.

During 1943 the windows were open but during 1944 they were kept closed. This made no difference to light but greatly cut down air-currents and temperature and humidity fluctuations. The grain temperature at a depth of one foot was measured at two places. It was very uniform owing to the low conductivity of grain. The air temperature was relatively uniform since it was controlled by that of the grain, especially when the windows were shut. It was measured by a thermograph near the centre of the room. The instrument had to be enclosed in a linen bag to keep out mice and insects.

The grain came into the room at a water content of 13.0-14.5% (based on wet weight), corresponding to a relative humidity of 67%. The average humidity of London air is somewhat higher than this, so that towards the end of the season a gradient in water content is set up in the bulk, mainly in the surface 30 cm. The relative humidity of the space between the grain and the ceiling was relatively constant, especially when the windows were closed. It was measured on a hygrograph (incorporated with the thermograph) and also occasionally with a whirling psychrometer.

¹ The wheat in 1943 was introduced into the empty room on 20.vi.

A figure of the number of grains in a given weight of grain was required as shown on p. 271. This was obtained on several occasions by weighing a number of samples of 100 grains, see Table 1.

TABLE 1.

Size of room = $50 \times 100 = 5000$ sq. ft. Height = 8 ft. Volume = 40,000 cu. ft.

Quantities of grain: 1943, 498.2 tons No. 2 N. Manitoba; 1944, 322.1 tons No. 2, 197.3 tons No. 1 N. Manitoba.

Surface of grain: 1943, 5250 sq. ft.; 1944 (two bulks), 5350 sq. ft.

Mean depth of grain: 1943, 56.3 in. (143 cm.); 1944, 58.7 in. (149 cm.).

Average wt. of 100 grains (twenty samples): 1943 = 2.895 g.; 1944 = 2.884 g.

No. of grains in room: 1943, about 1749×10^7 ; 1944, about 1823×10^7 .

Water content of grain.

1943. 4.xi. 5 cm. 15 cm. 25 cm. 50 cm. 100 cm.

(Mean of 3 sites)

W.C., % 15.6 14.5 14.0 13.9 14.0

R.H., % 75 72 70 69 70

1944. 11.iv. When grain was freshly placed.

Surface. Larger bulk: W.C. 13.96%; smaller bulk, W.C. 14.69%.

R.H. 69% R.H. 73%

Average Grain temperature in ° C. at 1 ft.												
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1943	—	—	—	—	—	15.25	16.45	18.5	16.75	14.35	10.8	—
1944	—	6.5	—	—	12.25	14	16	20	18.5	15	11	7
Average Air temperature in ° C. and R.H.												
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1943 Temp.	—	—	—	—	15	16.1	15.4	16.2	15.5	15.3	9.9	—
R.H., %	—	—	—	—	60	61.7	63.2	66.2	61.4	67.8	64	—
1944 Temp.	8	5	9	12.5	14.7	17.7	17.8	20.4	18	14.1	10.7	9
R.H., %	61	—	—	64	58.8	66.2	72.1	72	69.5	66	68.6	73
Light range in F.C.				> 1.0		0.9-0.1		0.09-0.01		0.009-0.001		0.0009-0
Area of room with this light intensity:												
1943				16%		27%		15%		21%		21%
1944				3%		9%		14%		62%		12%

Although air temperatures and humidities and grain temperatures were regularly measured, it was not found possible to relate them in any simple way to the changes in the insect population. We have therefore only included the monthly averages in the data in Table 1. When the windows of the room were closed in 1944, the daily range in temperature and humidity was considerably less than in 1943, when they were open. From May to November the temperature range was about 4.0-6.0° C. in 1943 and daily 1.0-3.5° C. in 1944; the daily range in relative humidity was about 15-35% in 1943 and about 3-15% in 1944. The daily range of temperature in the grain never exceeded 1° C. The environment is therefore an extraordinarily uniform one for a terrestrial animal and provides an unusual opportunity for making estimates of an insect population.

3. LIFE-HISTORY OF THE MOTH IN THE WAREHOUSE.

There is an endemic population which spends the winter as resting larvae in crevices, about 90% between the ceiling boards, but some also in cracks in pillars, pipes and walls. Very few spin their winter cocoons in the grain. At no time has Canadian wheat been found to enter the warehouse infested with *E. elutella*. The larvae in the crevices start pupating at the beginning of May and continue to do so throughout the summer, but the peak of pupation is at the beginning of June. Under warehouse conditions, the pupal period lasts 3-4 weeks, depending on temperature, *i.e.* shorter later in the summer. The moths, apart from very rare stragglers, start appearing at the end of May and the population of adults quickly reaches a maximum in the first fortnight of July; after that the numbers fall rapidly, but small numbers are present until the beginning of September. After this, there was in both 1943 and 1944 a very small overlapping second generation of moths, lasting until November or December.

The moths pair soon after emergence and usually pair several times during their life. Females lay most of their eggs in the first four days of their life. Moths usually live 2-3 weeks, depending on temperature and the size of the moths; males are rather shorter-lived than females. The eggs must nearly all be laid on the surface of the grain, for laboratory experiments have shown that this is an oviposition-site much preferred to wood, brick, etc. The larvae hatch in 10-14 days at normal summer temperatures and begin feeding on the wheat embryos. Dendy and Elkington (1919) first showed that in hard wheats only the embryo is eaten and that most of the damage is done to the surface layers. Damage caused by *E. elutella* on wheat has also been recorded by Zacher (1941), Munro (1940). A study (*Trans. R. ent. Soc. Lond.* 97) has been made of the behaviour of feeding larvae in the grain but the following facts are sufficient for present purposes. Most damage is done to the top 30 cm. of grain, but a few larvae penetrate as deep as 2 m. After the first two instars which are spent inside an embryo, the larvae progress from grain to grain, eating up the embryos. On the average, 48 embryos are eaten during larval development. The penetration of larvae can be determined by counting the number of damaged embryos, and data obtained in this way have been supported by the finding of larvae and their cast head-capsules in deep samples removed with a sampling spear. As the larvae approach the end of the feeding period (usually in the sixth, sometimes in the fifth instar), they gradually return to the surface and enter the wandering phase. Wandering larvae are first seen about 20th August and the biggest number is seen between 3rd and 20th September. The larvae wander for a variable period, most of them reaching the ceiling, and then enter a crevice to spin up for the winter. While wandering, they spin silk which forms continuous sheets on top of the grain, walls and ceilings when the larvae are numerous. A few of the earliest wanderers pupate at once and give rise to the slight second emergence in September-October, but the vast majority spend the winter as a resting last instar larva. Few larvae are to be seen by the beginning of November.

The eggs laid by the first of second generation of moths (later laid eggs are sterile) hatch and grow very slowly during the autumn. If the winter is not very severe, many of them grow slowly throughout the winter and pupate rather later than the overwintering larvae.

4. ESTIMATION OF NUMBERS OF ADULTS.

The number of moths present in the room from week to week was estimated by counts on regular sampling areas (see Table 2).

It was unnecessary to count flying moths as the vast majority were always at rest in the daytime.

In 1944, 18 muslin bags were fixed over strips of ceiling crevices about 2 ft.

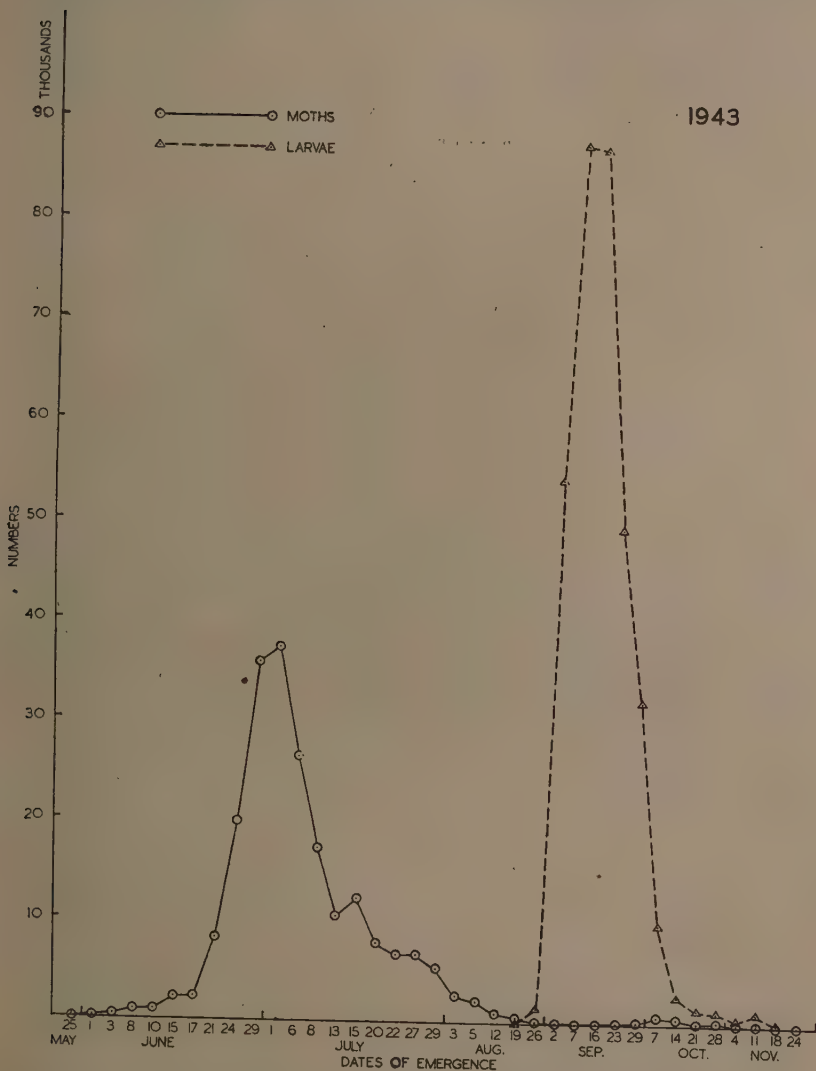


FIG. 1.—Dates of emergence of moths and larvae in 1943 (Counts, mostly twice a week).

long, on 10th May, so as to catch all the moths emerging from 1.16% of the ceiling, *i.e.* about 1.13% of all moths. These bags were emptied once a week and this gave an estimate for the seasonal emergence curve as well as for the accumulated total of moths.

When moths die their bodies lie on the grain and these were counted on a number of 1-sq. ft. areas. In 1943 the areas were trays of grain exposed for the estimation of oviposition. It appeared later that moths did not often die on the trays, perhaps because the edge of the tray formed a barrier to a dying moth crawling on the grain. The total number of dead moths found was very small. Moreover, in 1943, the windows of the room were open and it appeared that many moths flew out, particularly when they began to age and to lose their negative reaction to light.

TABLE 2.

Sample areas for moth and larval counts.

Type of surface	No. of sampling areas	Sampling areas as % of total area
Walls	12	8.0
Bulkhead	2	10.0
Windows	3	33.3
Pipes	4	11.0
Pillars	4	12.5
Beams	4	11.0
Ceiling { 1943	5	1.5
{ 1944	10	4.5
Grain	2	10.0

In 1944, dead moths were collected on 20 foot-square areas of grain (0.4% of total grain surface) towards the end of emergence. The windows were closed this year and the estimate of dead moth numbers showed reasonable agreement with the estimates based on the weekly counts.

The weekly count of moths on the sampling areas could only be converted into an accumulated total if the length of life of the moths was known. As the sexes differ in length of life and have to be treated separately, it is necessary to know the sex-ratio, at least if it is not 1 : 1.

In 1943, the sex-ratio based on 1008 live moths caught in various parts of the room was 610 ♀ : 398 ♂ = 3 : 2. In 1944, 790 live moths were 472 ♀ : 318 ♂ and the dead moths 850 ♀ : 854 ♂. For calculations, the sex-ratio in 1943 has been assumed to be 3 ♀ : 2 ♂ and 1944 : 1 ♀ : 1 ♂. The excess of live females in 1944 may have been due to the longer life of that sex, together with the accident that more moths were collected in the second half of the season.

The average lengths of life in 1943 were (see Appendix 1) ♂, 19.9, ♀, 23.4; 2 ♂, 3 ♀, 22.0 days. In 1944, ♂ 11.5, ♀ 13.5; 1 ♂, 1 ♀, 12.5 days.

The number of moths counted on the sampling areas each week can be plotted on a curve. At the start all moths are newly emerged. By taking successive periods equal to the length of life, by a series of subtractions from the curve, the numbers of newly emerged moths can be read off each week; the sum of successive batches of newly emerged moths gives the accumulated total (see Table 3). The number of moths dying in any period is also calculated from the emergence curve using the length of life (see Appendix 2).

This method worked well in 1944, when the windows were closed and the

TABLE 3.

Moth counts, moth emergence, etc., in 1943 and 1944. Counts to the nearest hundred.

1943		1944		Calculated on assumption, mean length life = 12.5 days			Moths emerged since last date, estimate based on emergence in muslin bags
Date	Total moths present. Estimate from sampling areas	Date	Total moths present. Estimate from sampling areas	New moths since last date	Moths from previous dates	Moths died since last date	
25.v.	[30]	5.v.	200	200	0	0	—
1.vi.	200	10.v.	300	100	200	0	Bags put up
3.vi.	480	—	—	—	—	—	—
8.vi.	900	17.v.	400	300	100	200	0
10.vi.	980	—	—	—	—	—	—
15.vi.	2,100	24.v.	200	0	200	200	100
17.vi.	2,300	—	—	—	—	—	—
21.vi.	8,200	31.v.	600	600	0	200	0
24.vi.	19,800	—	—	—	—	—	—
29.vi.	35,800	6.vi.	900	343	557	43	0
1.vii.	37,300	—	—	—	—	—	—
6.vii.	26,400	14.vi.	900	643	257	643	0
8.vii.	17,300	—	—	—	—	—	—
13.vii.	10,500	21.vi.	1,300	858	442	458	200
15.vii.	12,200	—	—	—	—	—	—
20.vii.	7,800	29.vi.	10,100	9,548	552	748	15,600
22.vii.	6,700	—	—	—	—	—	—
27.vii.	6,700	6.vii.	125,500	118,936	6,564	3,536	140,400
29.vii.	5,400	—	—	—	—	—	—
3.viii.	2,600	12.vii.	197,500	87,059	110,441	15,059	95,600
5.viii.	2,100	—	—	—	—	—	—
12.viii.	1,000	19.vii.	136,300	56,496	79,804	117,696	53,100
19.viii.	600	25.vii.	72,400	19,939	52,461	83,839	28,200
26.viii.	100	1.viii.	30,800	12,523	18,277	54,123	16,500
2.ix.	(70)	9.viii.	11,800	3,750	8,050	22,750	4,300
		17.viii.	3,100	991	2,109	9,691	2,500
		24.viii.	1,000	318	682	2,418	900
		31.viii.	400	150	250	750	100
		7.ix.	100	0	118	282	100
		Totals	—	312,754	—	312,636	357,600

1943

Accumulated total of moths, calculated as
in Appendix 2 = A = 59,700.

Maximum moth numbers (1.vii.) = 37,300
= B. A/B = 1.60.

No. of ♀ = $\frac{3}{5}$ A = 35,800.

1944

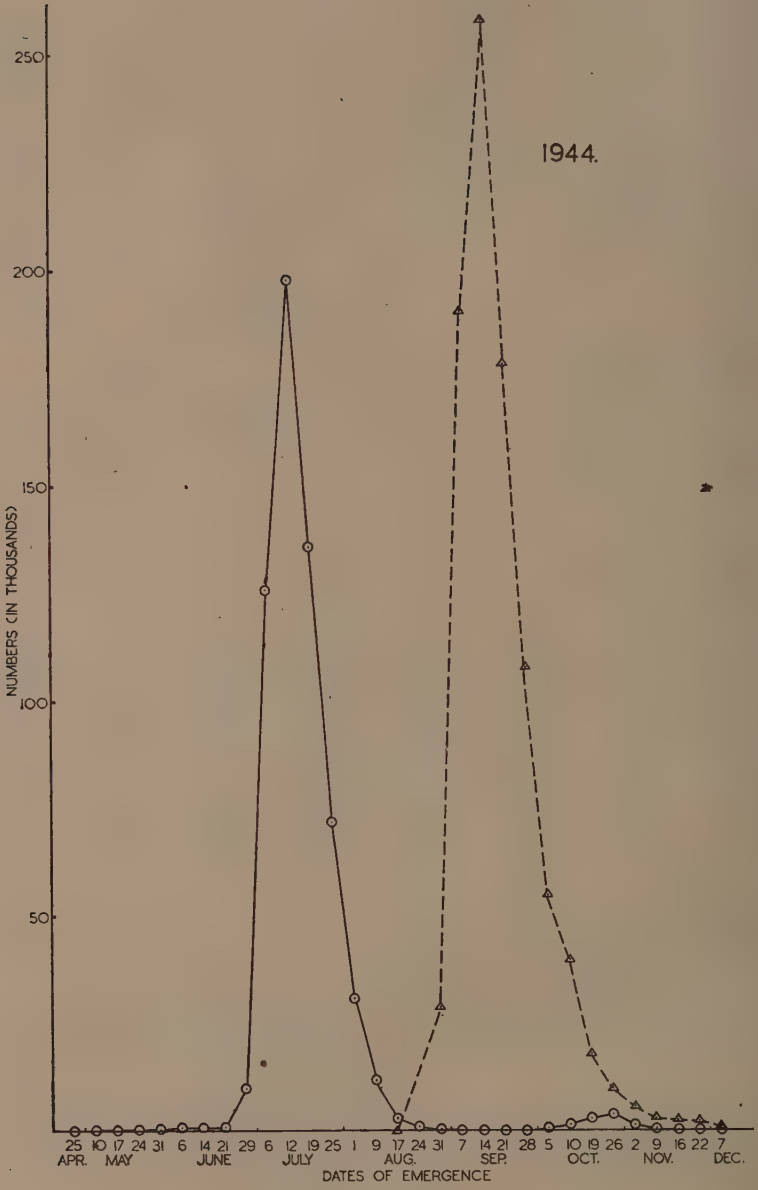
Accumulated total of moths, calculated
from sample counts on basis of length of
life of 12.0 days = 336,280.

Estimated no. of dead moths on 24.viii.
based on counts on 20 1-ft. squares =
285,160 = D.

Dead moths expected on this date from
column 7 = 311,604. A = 312,800.

B = 197,500. A/B = 1.58.

No. of ♀ = $\frac{1}{2}$ A = 156,400.



2

FIG. 2.—Dates of emergence of moths and larvae in 1944 (Weekly counts).

accumulated total of moths agreed with estimated number of dead moths and when there was a check on the emergence from the numbers in the muslin bags.

In 1943, when the windows were open, the numbers found in the room fell much more rapidly after the peak of emergence than could be accounted for by the normal death-rate. It is certain that very large numbers flew out of the windows; this was observed to be happening on 15.vii.43 when between 7.20 and 7.50 p.m. G.M.T. about 43 moths flew out and 11 flew in at one of the nine windows. The weekly moth totals for 1943 are given in Table 3, but the estimate of the accumulated total was arrived at by an argument given in Appendix 2. Data of oviposition suggest that this total is not far from the true one.

The following points in Table 3 call for comment. In 1944, there was a small preliminary emergence (5.v.-24.v.) which was really distinct from the main emergence. Many of these moths were found in one corner of the room but no reason was found why there should have been an earlier emergence there.

It is not clear why the estimates based on emergence in the muslin bags tend to be higher than those calculated from the weekly moth counts. It is possible that the bags did not cover a random sample of the ceiling, but calculating the standard deviation from the mean number per bag and taking the true mean to lie within twice the standard error of the actual mean, the limits of the accumulated total based on bag-counts are 341,500 and 374,700. As shown at the bottom of Table 3, the accumulated total calculated from the weekly moth counts would be as large as 336,280 if the length of life were taken as 12.0, not 12.5 days. However, for purposes of calculating oviposition and the expected number of larvae, the figure of 313,000 moths, of which half were females, has been used.

On two occasions in 1943, moth counts were made twice in one day and though the numbers in the individual sample areas varied considerably, the estimated totals for the whole room agreed within 5%.

Date	Count at		Count at		% difference of later count
15.vii	2.15 p.m.	12,240	8.45 p.m.	12,015	-1.8
29.vii	9.30 a.m.	5,358	1.30 p.m.	5,612	+4.8

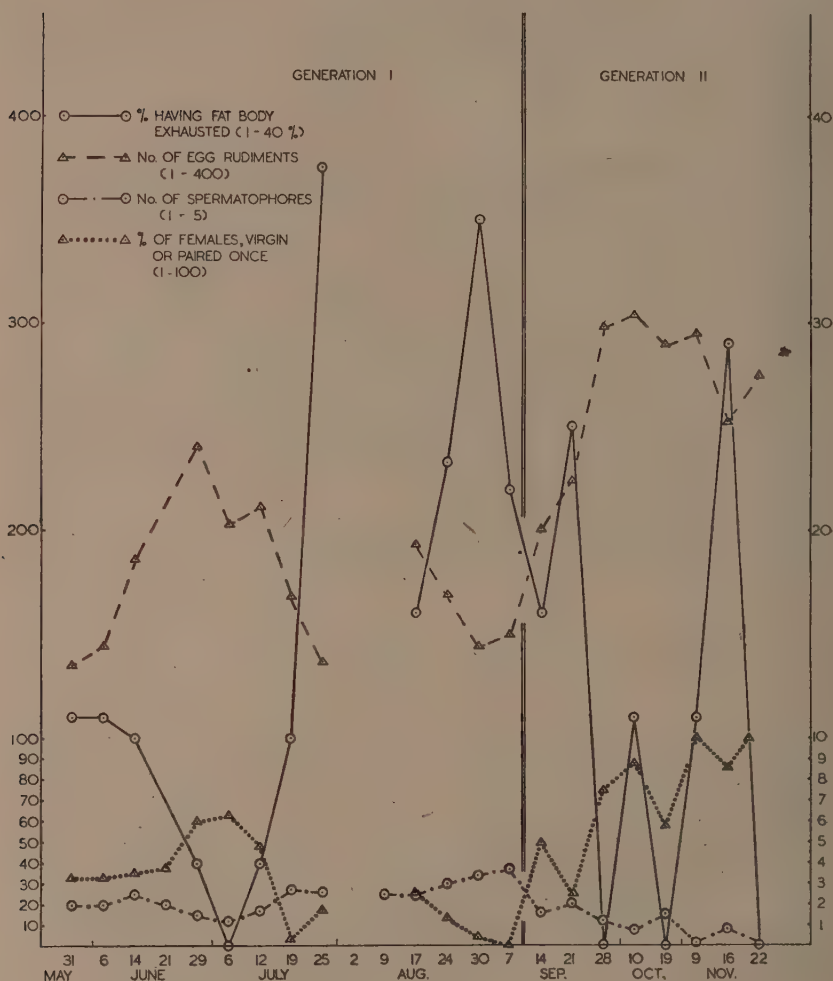
It is not unexpected that the estimate of dead moths was somewhat low, for not only may a few moths have escaped from the room but in the period 21.vi.-24.viii. a number of dead bodies may have been destroyed by mice or insects (e.g. *Ephestia* larvae or *Ptinus tectus*). For both 1943 and 1944, the ratio (A/B in Table 3) has been calculated between the estimate of the complete emergence of moths (= accumulated total) and the highest number seen on any one date. If it could be shown that under British conditions this ratio was always in the neighbourhood of 1.6,² it would provide a useful practical guide. It would often be useful to be able to say from, perhaps, two successive counts that the accumulated total lay between the larger of the two counts and a number twice as large.

In 1944, samples of moths were brought back each week and dissected by Mrs. M. J. Richards on the day after that of capture (cf. Norris 1933, 1934). She recorded the following data for each batch: (a) percentage having the fat-body exhausted, (b) the average number of egg-rudiments, (c) percentage of

² The value for the room 2 which was sprayed (App. 2, p. 293) appears to be about 1.60.

females unpaired or paired only once, (d) average number of spermatophores per female.

(a) and (b) give a rough measure of the age of the population. (c) and (d) are similar measures, for as the females get older, they pair again and eventually as many as seven spermatophores may be found in the bursa copulatrix of a single female. The data are shown in fig. 3; the number of moths dissected



3

FIG. 3.—Dissection of female moths collected in the granary 31.v.-22.xi.44 (M. J. Richards). (a) $\circ$ — $\circ$, percentage of females with fat-body exhausted. (b) $\triangle$ — $\triangle$, average number of egg-rudiments per female. (c) $\triangle$ $\triangle$, percentage of females unpaired or paired only once. (d) $\circ$ $\circ$, average number of spermatophores per female.

was 437, about 15 in each batch. It will be noticed that the peak in number of egg-rudiments and in number of females which have paired less than twice occurs on 29.vi.-6.vii. when, from Table 3, the number of new moths (moths <7 days old) exceeds the number of old moths (>7 days) by 17-18 times, whereas the ratio of new to old moths later in the season is 0.4-0.7.

Apart from the anomalous early emergence in May 1944,³ the peak of moth numbers seems to have been about ten days later in 1944 than in 1943. Owing to a difference in the length of life in the two years, the real difference in the peak of emergence in the two years was about a week. In 1943, counts of moth numbers were made in two other rooms and in both of these the peak of moth numbers came on the same date as in the main room. In a fourth room, however, temperature conditions were very different owing to the heating of the English oats which it contained. The hottest part of the oats was 38.9° C. (unheated parts 16.0° C.) and the air above the oats varied in temperature from 19.3 to 22° C. (on 8.vi.). In this room, there were 4000 moths on 18.v.43, and clearly the emergence in this room had been accelerated by 2-4 weeks.

Wandering larvae of the autumn of 1943 were kept in tins in an unheated outhouse at Slough. The peak emergence of moths from these larvae (see Table 14) was on the same date as in the warehouse, but the peak was not so sharp and the main emergence was spread over a longer period.

The period of emergence in the London region seems to be relatively fixed and exceptional climatic variation is required to alter it by more than a few days.

5. ESTIMATION OF NUMBERS OF EGGS.

If the number of eggs laid by an average female moth and the number of such moths are known, then it is possible to calculate the number of eggs which will be laid per square foot on a known surface of grain.

In 1943, the fecundity (= number of eggs per female) was recorded for the 526 ♀ which were isolated in tubes in the warehouse throughout the season (Appendix 1, p. 291). As in estimating the length of life, the number of eggs observed was doubled to get the true value which came to 124 eggs per female for the first generation. When a sample of females is isolated each week, it is also possible to estimate the number laid in that week without making any allowance for changes in the age of the population.

As shown in data published elsewhere (Waloff and Richards, *Trans. R. ent. Soc. Lond.* 97), the moths found in the lighter parts (>1.0 F.C.) of the room tend to be older than those found in darker parts (0.9-0.0 F.C.). Collections were made in areas of each type and the oviposition recorded separately. The figures obtained were: dark areas, 349 moths, 21,856 eggs, actual mean 62.6, true fecundity = 125.2. Light areas, 177 moths, 10,429 eggs, actual mean 58.9, true fecundity 117.8. The ratio of light to dark areas in the room was as 16:84. If the fecundities of the two lots of moths are taken in these proportions, the average figure for the whole room for the season is 124.0.

In 1944, fecundity was estimated more indirectly by methods given in Appendix 3. The figure for the season has been taken as 91.

A separate estimate of the number of eggs laid per square foot of grain was obtained by exposing 30 trays of grain. The trays were made of perforated zinc with a wooden frame. A square of muslin was laid on top of the zinc and

³ Nine females were dissected. There were 1-4, average 2.0, spermatophores in the bursa copulatrix, yet in only three moths were any sperm in the receptaculum. It seems as if these moths were in some way abnormal, at least in the male sex.

enough grain (200 g.) to form a layer one grain deep was poured on and spread out. The area of the grain on the trays was about 0.7 sq. feet, but a correction can be made to reduce them all to one square foot. The grain was taken from a part of the bulk which had been covered with a large sheet of cardboard at the beginning of the season. It was replaced every week and the grain with eggs was poured into jars and incubated for 21-28 days at 25° C., when the resulting larvae were big enough to count. The trays were distributed on the surface of the grain throughout the room, on the tops of grain-cones and in valleys and in areas of various light-intensity. They were exposed for 8 successive weeks from 24.vi. to 19.viii. The tray data provide an estimate of total as well as of weekly oviposition.

In 1944, 19 trays were exposed for two successive weeks at the time when moths were most abundant (6.vii.-19.vii.). In order to compare oviposition deduced from tray-records with that expected from the number of moths in the room the average number of moths present per day must be calculated. This was done as follows, taking the tray-week 24.vi.-1.vii. as an example.

$$\begin{aligned}\text{Moth count on } 24.\text{vi.} &= 19,780 = b + c \\ \text{,, } 29.\text{vi.} &= 35,780 = 6b + c. \\ b &= 3,200 \\ \text{Thus, number on } 24.\text{vi.} &= 19,780 \\ 25.\text{vi.} &= 22,900, \text{ etc.}\end{aligned}$$

A new calculation is made for the period 29.vi.-1.vii. The daily moth number was taken as the average of the first seven figures obtained by these calculations. Allowing for the sex-ratio of 3 ♀:2 ♂, $\frac{3}{5}$ of the daily number were taken as females.

The oviposition on the trays was compared with that of moths isolated each week in tubes. About half the moths were set up on the same day as the trays, so that their weekly oviposition-rate could be used directly. The rest of the moths were set up on another day of the week, but their oviposition-rate during the "tray-week" was calculated on the assumption of a uniform daily oviposition-rate, which is probably not far from the truth with a large batch of moths of mixed ages. All the data for 1943 are assembled in Table 4.

In 1944, 19 trays were exposed for thirteen days, 6.vii.-12.vii. and 12.vii.-19.vii., when the moths were at their maximum. As adequate data for the oviposition of moths in tubes were not recorded, an estimate of their expected oviposition was obtained in another way (see Appendix 2). These data are given in Table 5.

In Table 4, row 2 shows the number of eggs which would probably have given rise to the number of larvae obtained by incubating the "tray grain." The allowance for infertility of eggs and for mortality of larvae is calculated in Appendix 3. The figures for eggs laid on the trays enables the corresponding ones for eggs laid on the whole area of grain (Table 4, row 3) to be calculated. Table 4, row 4, gives the average daily number of females present in the room each week, calculated from the data in Table 3, by the method described on p. 293, and the average number of eggs laid by these moths per week (Table 4, row 5) is found by dividing the figures in row 3 by those in 4. The calculated oviposition-rate is then compared with that observed in females isolated in tubes kept in the warehouse (Table 4, row 6). The observed oviposition-rate is then converted to a figure for eggs laid on the whole area of grain (Table 4, row 7) by multiplying by the average number of females present. In row 9, the total number of eggs is divided by the ratio between the area of the grain and

TABLE 4.
1943. Larvae bred from 30 trays of grain and comparisons with oviposition expected from moth counts.

Week ending	1.vii.	8.vii.	15.vii.	22.vii.	29.vii.	5.viii.	12.viii.	19.viii.
1. Average no. of larvae per tray (after incubation)	84.1	69.3	46.9	38.0	19.3	12.9	3.7	3.1
2. No. of eggs which would have produced this no. of larvae, assuming 10% infert. of eggs and 25% larval mortality (i.e. $\times 1.48$)	124.5	102.6	69.4	56.2	28.6	19.1	5.5	4.6
3. No. of eggs added to the grain in the week (i.e. multiplying by area of grain/area trays = 7192.5)	895,500	738,000	499,200	404,200	205,700	137,400	39,600	33,100
4. Average no. of ♀ moths present in the room, daily each week	17,400	18,200	8,100	5,800	4,500	2,200	900	500
5. Calculated oviposition-rate, eggs per moth per week (dividing 3 by 4)	51.5	40.5	62.4	69.7	45.7	62.5	44.0	66.2
6. Eggs per week of ♀ isolated in tubes (no. of ♀ each week in brackets)	64 (44)	55 (55)	51 (50)	62 (61)	43 (55)	51 (49)	42 (59)	56 (15)
7. No. of eggs added to the grain in the week (multiplying figures in 6 by those in 4)	1,113,600	1,001,000	413,100	359,600	193,500	112,200	37,800	28,000
8. Difference between figures in (3) and those in (7), as a percentage of those in (3)	-24.4%	-35.6%	+17.2%	+11.0%	+5.9%	+18.4%	+4.5%	+15.4%
9. No. of eggs expected per tray per week, from no. of moths (4) and oviposition in tubes (6) (i.e. figs. in (7) divided by 7192.5) (compare with 2)	154.8	139.1	57.5	50.0	26.9	15.6	5.3	3.9

Total no. of eggs laid on the grain 24.vi.-19.viii.

A (based on 3) = 2,952,700. A + C = 3,288,200.
 B (based on 7) = 3,381,200. B + C = 3,716,700.
 D. Estimate for egg-number actually used =
 = 3,715,000 + 1,001,000 + 13.3% + sum of 499,200 . . . 33,100 + C.
 = 4,050,500. First stage larvae, take off 10% (= 405,050) = 3,645,450.

No. of eggs laid 20.vi.-24.vi. 323,400
19.viii.-2.ix. 12,100

335,500 = C
E. Estimate of egg-number based on total number of females 35,800 (Table 3) and an average fecundity of 124.0 = 4,439,200.

the area of the trays. This gives a set of figures to compare with those in row 2. Finally, in row 8, the difference between the two estimates of total number of eggs laid per week is expressed as a percentage of that derived from the trays (row 2).

It will be noticed that the estimates based on the trays for the first two weeks are considerably lower than those based on "tube" oviposition records, whereas for the last six weeks they are consistently higher. The discrepancy in the first two weeks is certainly due to overcrowding of the larvae during incubation. As shown later (p. 283) overcrowding above 1 larva per 5.0 g. increases the mortality above the 25% which we have allowed. Even if the estimates of 125 and 103 eggs laid on the trays were correct, the resulting larvae would only have had about 2.0 g. each.

TABLE 5.

1944 larvae bred from 19 trays and comparisons with oviposition expected from moth counts.

Tray periods, 1944	6.vii.-12.vii.	12.vii.-19.vii.
1. Average number of larvae per tray (after incubation)	338.3	310.5
2. No. of eggs which would have produced this number of larvae, assuming 10% infertility of eggs and 25% larval mortality (i.e. $\times 1.48$)	500.6	459.5
3. No. of eggs laid on the grain in the period (i.e. multiplying by the area of the grain divided by the area of tray = 7329.5)	3,669,100	3,367,900
4. Oviposition of moths during the period, calculated as in Appendix 2	4,030,500	3,501,700
5. Expected no. of eggs per tray, i.e. figures in 4 divided by 7329.5 (cf. 2)	550	478
6. Difference between figures in 3 and those in 4 as a percentage of those in 3	-9.8%	-4.0%
Accumulated total of moths (Table 3)	5.v.-7.ix. 312,800	
Number of ♀ moths. Sex ratio 1:1	156,400	
No. of eggs. Fecundity (p. 296) = 91	14,232,400	
No. of first stage larvae, take off 10%	12,809,200	

From the data in Table 4, an estimate is made of the number of larvae to be expected in the whole room. First, additions have to be made for oviposition from 20.vi. (when the grain was put in the room) to 24.vi., and from 19.viii.-2.ix., the end of the first generation of moths. These estimates were obtained in the same way as those in Table 4, row 7. Next, it was decided that the estimates of egg-numbers based on the trays were more likely to be accurate than those calculated in row 7, except for the first two tray-weeks. This was because the thirty trays provided a reasonably large sample area and the moths laying on them are a large population, not a small sample isolated in tubes. For the first two tray-weeks a figure was obtained by adding to the two estimates in row 7 an allowance of 13.3%, which is the average amount by which tray estimates exceed those in row 7, over the last six weeks. These calculations are shown at the bottom of Table 4, and give a total of 4,050,500 eggs. A similar estimate based on the total number of female moths with a fecundity of 124.0 is also given in the table (4,439,200). The excess in this estimate may be due to some females flying out of the windows before completing oviposition.

In 1944, in order to avoid overcrowding of larvae, the grain from the trays was diluted from 200 g. to 2240 g. before incubation. According to the figures in Table 5, the larvae should have had more than 4.0 g. of grain each.

To compare with the figures for the number of eggs laid on the whole area of grain (Table 5, row 3), a second figure was calculated, based on the number of females of various ages and the number of eggs which they would lay at that age, as described in Appendix 2. From these, a second figure for eggs per tray can be calculated. The calculated figures are in both weeks somewhat (4-10%) higher than those expected from the tray records. In view of the assumptions involved in the calculations, a better agreement could hardly be expected.

Finally, using the figure for the accumulated total of moths from 5.v.-7.ix.44 given in Table 3, an estimate was made of the number of eggs to be expected in 1944, viz., 14,232,400.

If the average excess of the two calculated estimates over the two tray estimates is worked out, it gives a figure of 6.6%. If this is taken off the larval estimate, it gives a second egg estimate of 13,294,000.

6. ESTIMATION OF NUMBERS OF LARVAE.

No attempt was made to estimate the size of the population of feeding larvae. It is difficult to find 1st and 2nd stage larvae in grain, but most of them will appear if the grain is soaked in 30-50% alcohol. They then come out of hollow embryos and mostly float to the surface. In 1943, from 29.vi.-29.ix. four weekly samples each of 400 g. were taken from four different spots

TABLE 6.

Development of larvae in grain in 1943. On each date four samples, each 400 g., were taken.

Date	Eggs	Stage I	Stage II	Stage III	Stage IV	Stage V	Stage VI
29.vi.	Many	—	—	—	—	—	—
6.vii.	Some	7	—	—	—	—	—
20.vii.	None found	13	8	1	—	—	—
27.vii.	" "	—	9	13	—	—	—
3.viii.	" "	—	4	21	13	—	—
10.viii.	" "	—	3	8	15	9	—
19.viii.	" "	2	5	10	13	19	9
26.viii.	" "	—	1	1	4	15	16
2.ix.	" "	—	2	2	2	9	59
9.ix.	" "	—	—	—	2	2	13
16.ix.	" "	—	—	—	—	8	12
23.ix.	" "	—	—	—	—	1	6
29.ix.	" "	—	—	—	—	2	—

and examined for larvae. The figures (Table 6) give a picture of the development of the population but probably no reliable estimate of its size.

When fully fed, the larvae leave the grain, wandering over its surface, and most of them eventually reach the ceiling. At this time they can be counted just like the moths and on the same sample areas. In 1943, the first two wandering larvae were seen on 19.viii. and their numbers were large by 2.ix. Greatest numbers were present during 9-16.ix. In 1944, two wandering larvae were seen on 17.viii., moderate numbers were present on 31.viii. and greatest numbers on 14.ix.

The number of larvae visible on any day is the resultant of the number leaving the grain and the number entering crevices to hibernate. In order therefore to interpret the weekly larval counts, it is necessary to know the average time spent in wandering before entering a crevice. The length of the wandering period plays the same part in calculations as the length of life in the moths.

The average length of the wandering period was measured by marking larvae with cellulose paints. The larvae were marked after they had reached the ceiling. Some small-scale observations suggested that most larvae reached the ceiling in a very few hours. Although wandering larvae may travel 50 ft. or so, most of them seem to stay within a confined area. The marking and the later searching for marked larvae was done in one corner of the room. To mark larvae at random and then search the whole room for them was impossible in the time available.

In 1943, larvae were marked on 29.ix., 7.x. and 14.x. and were also looked for on 21.x. and 28.x. The weekly interval was found to be too long and in 1944 more frequent counts were made, mostly at two-day intervals. The results of this work are given in Table 7. The average length of the wandering period is

TABLE 7.
Recovery of marked larvae in 1943 and 1944.

Date, 1943	No. of larvae marked	Per cent. recovered on—			
		7th day	14th day	21st day	28th day
29.ix.	327 = 100%	7.3	1.5	1.5	0.6
7.x.	299 = "	5.3	2.6	0.7	—
14.x.	137 = "	4.4	2.9	—	—
Average	100%	5.7	2.3	1.1	0.6

Date, 1944	No. of larvae marked	Per cent. recovered on the following days											
		2	5	7	9	12	14	16	19	21	23	28	30
21.ix.	649 = 100%	—	—	1.23	1.08	0.31	0.31	—	0.15	0	—	0	0
28.ix.	487 = "	9.45	3.69	1.23	—	0.62	0.62	—	—	0.2	—	0.2	0
3.x.	299 = "	6.69	—	1.67	1.67	—	—	1.0	—	—	0.66	—	0
Average	100%	8.07	3.69	1.38	1.38	0.47	0.47	1.0	0.15	0.1	0.66	0.1	0

obtained by drawing a curve relating percentage recovery to time since marking (see fig. 4). The area beneath this curve (measured with a planimeter) divided by the length of the initial ordinate (A-B in fig. 4) gives the mean length of the wandering period. The result is much affected by the way the curve is drawn and it would have been better in each year to have searched for marked larvae at more frequent intervals. In 1943, when the value was unknown, this could not be helped and in 1944 the wandering period appears to have been shorter so that two-day intervals were still too long. The lengths of the wandering period estimated in this way was 56 hours in 1943 and 24.5 hours in 1944.

These results are used to turn the weekly estimates of numbers of larvae visible into accumulated totals. Assuming that the numbers of larvae can be averaged over a week, the average number which would have been seen on each day of, for example, the week 2.ix.-9.ix.43 would have been $\frac{544 + 875}{2} 10^2$.

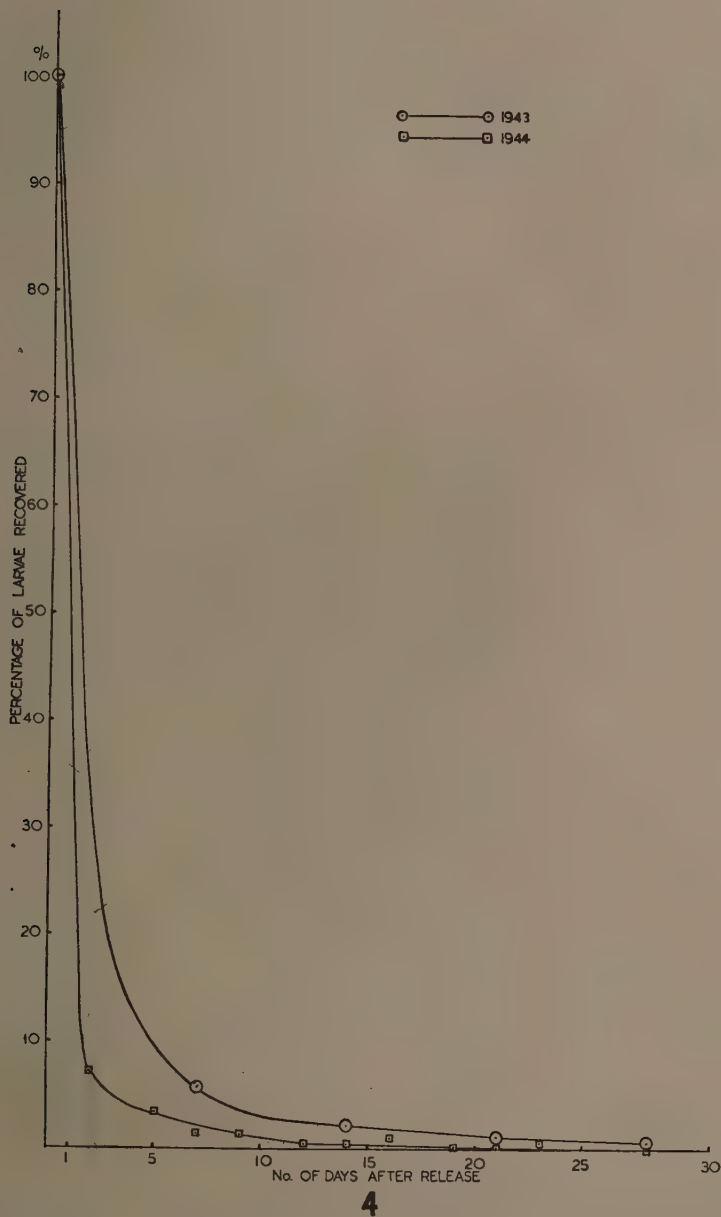


FIG. 4.—Curves relating percentage recovery of marked larvae to number of days after their release, 1943-44.

The week being divisible into three wandering periods ($3 \times 56 = 168$ hrs. = 1 week), there would have been $3 \times \frac{544 + 875}{2} 10^3$ in the week. The accumulated total for the whole thirteen weeks obtained in this way works out at a figure very nearly the same as the sum of all the weekly counts multiplied by $\frac{168 \text{ hours}}{56 \text{ hours}}$. This latter method of calculation has been used. For 1944, the total

of larvae seen on the thirteen counts has been multiplied by $\frac{168}{24.5}$. From these calculations, the estimated number of wandering larvae in 1943 and 1944 was 989,500 and 6,165,600. Before discussing the discrepancy between these figures and those in Tables 4 and 5, it is convenient to give a third estimate of the number of larvae based on the amount of damage done to the grain.

As explained on p. 256, the larvae eat only the embryo of hard wheat. Many other insects also eat wheat embryo but of these only *Ptinus tectus* Boield. (Col., PTINIDAE) was present in sufficient numbers in the room to have any importance. In grains damaged by *Ptinus* the part eaten out has a rounded edge and typically more of the pericarp which covered the embryo is left uneaten. Damaged grains were first sorted from whole ones and then re-examined and those probably due to *Ptinus* damage were eliminated. This can be done with only a small margin of error.

The number of wheat embryos eaten by one *Ephestia* larva in its development was determined at 25°, 21° and 17° C. at 70% R.H. using No. 1 Manitoba wheat. Seventy-five larvae were started at each temperature but the numbers surviving to spin up were 66, 68 and 49. The average numbers of embryos eaten was 47, 49 and 46. As there seemed to be no obvious temperature effect, the total number of embryos (8731) eaten was divided by the total number of larvae (183) and this gave an average figure of 47.71 with a standard error of ± 1.04 .

In order to estimate the number of *Ephestia*-damaged wheat grains in the warehouse, samples were taken from 30 spots scattered over the room. At each spot samples of about 25 g. were taken with a sampling spear (Oxley & Henderson, 1944) at depths of 0, 8.0, 25.0, 50.0, 100.0 cm. (in 1944, also at 75.0 cm.) and where this was possible a further deeper sample (125.0–175.0 cm.). Subsamples of 500 grains were taken from the spear-samples and the number of eaten embryos was counted and expressed as a percentage. The percentage damage was then plotted against depth (fig. 5) and the area beneath the curve was measured with a planimeter. The area divided by the initial ordinate (AB in the fig. = average depths of grain, given in Table 1) gave the average percentage damage, which was 1.30% in xi.1943 and 2.60% on 9.xi.44. Unfortunately, these figures cannot be expected to give a very accurate estimate of larval numbers for the following reasons. (1) The graphical method of determining average damage is not very accurate. Thus the figure for 1943 given as 1.30% might lie anywhere between 1.25 and 1.35%, giving an estimate of larval numbers lying between 4.58 and 4.94 millions. (2) As is shown on p. 283, the density of larvae feeding on a given bulk of grain affects the weight of the last instar larvae produced. It appears that larvae the weight of which is reduced by crowding eat fewer embryos. The figure of 47.71 embryos per larva is only true of larvae reared singly on an excess of grain (150 grains per larva). (3) The majority of the embryos eaten are consumed in the last instar, e.g. in larvae with six instars about three-quarters of all the embryos destroyed are eaten in the sixth instar. Thus if there is considerable larval mortality,

the estimate of larval numbers based on damage is much affected. The larval estimate will be a minimum for larvae of all stages but a maximum for wandering larvae which have ceased feeding.

However, by taking the figures of 1.30% damage for 1943 and 2.60% for 1944 and taking the figures for the numbers of the grains in the bulk in each year (Table 1), an estimate could be made of the total number of damaged embryos. This divided by 47.71 gave estimates of the number of larvae which were 4,765,700 in 1943 and 9,934,600 in 1944.

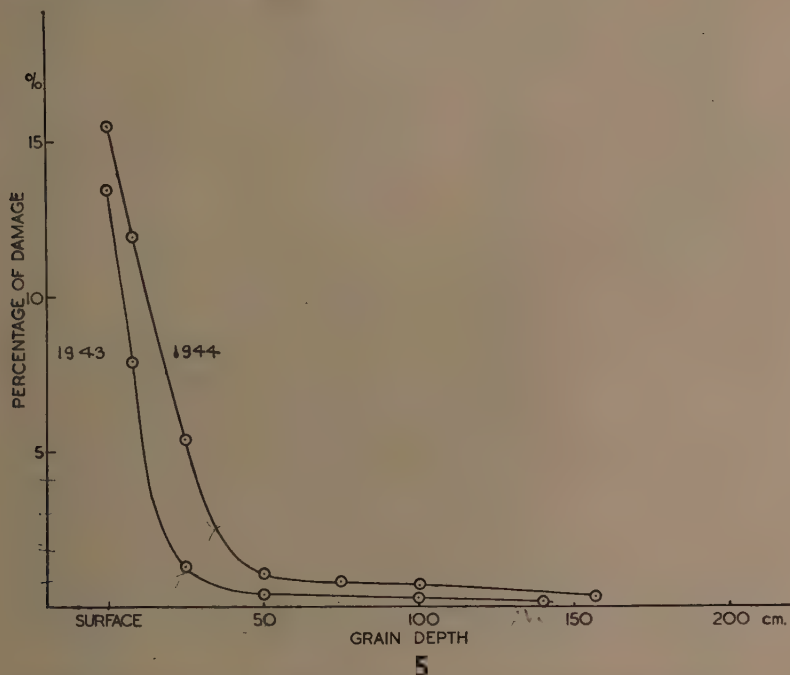


FIG. 5.—Curves relating percentage of damaged grain-embryos to depth in the bulk, 1943-44.

The principal cause of larval mortality is a bacterial disease which Dr. S. E. Jacobs informs us is probably due to a non-spore-forming bacillus, *i.e.* not of the type of *B. thuringiensis* Berliner. We refer to this disease as wilt. It causes larvae to liquefy and eventually to blacken and dry up. The wandering larvae were the stage most obviously attacked but according to Dr. Jacobs such diseases are also very fatal to younger larvae. The data in Table 17 also show that small, though fully fed, larvae are more likely to die than larger ones.

The mortality of the larvae from wilt can be divided into three parts, (1) death of feeding larvae, (2) deaths of wandering larvae and (3) deaths of larvae spun up in crevices. In 1943, an estimate was obtained of (2) and (3) but in 1944 (1) was also estimated.

The estimate of dead larvae in grain was obtained on 9.xi.44 by taking 30 spear-samples at depths of 0, 8.0, 25.0, 50.0, 75.0 and 100.0 cm. A further 13

were taken at depths >100.0 cm. where the grain was deep enough. A second lot of 30 larger samples at 25.0 cm. was taken on 7.xii.44 in order to obtain more larvae which could be placed in their instars. The samples were not of identical weight but the figures are expressed in the Table as larvae per lb. From the figures of larvae per lb. up to 50 cm. (no dead larvae were found below 50.0 cm.), fig. 6 was drawn and dividing the area beneath the curve by the abscissa (50) gives a mean of 10.4 dead larvae per lb. in the top 50 cm. The

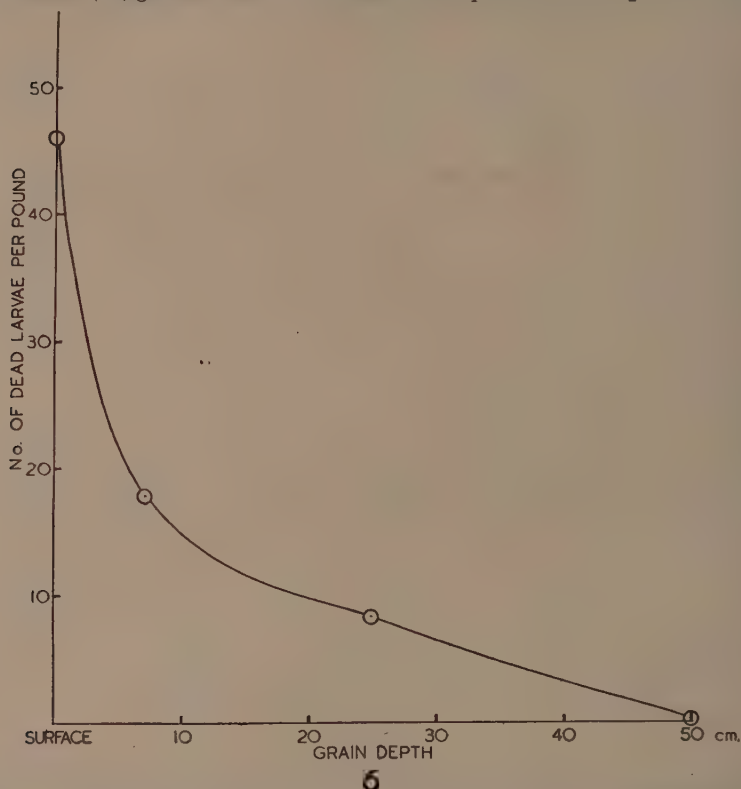


FIG. 6.—Curve relating number of dead larvae per pound of grain to depth in the bulk, 1944.

mean depth of the bulk was 149 cm. so that in the bulk of 519.4 tons, there were

$$519.4 \times \frac{50}{149} \times 2240 \times 10.4 = 4,060,400 \text{ dead larvae.}$$

The dead larvae found in the set of samples at 25.0 cm. on 7.xii. fell into the following instars:—6th, 50; 5th, 39; 4th, 13; 3rd, 2. Presumably small larvae which have died of wilt are so difficult to find that they have been overlooked. As the lengths of the instars vary between 6 and 15 days, provided all instars are equally susceptible, they might be expected to die in the grain in not very different proportions, so that the absence of the earlier instars is probably due to failure to find them.

The most conspicuous mortality from wilt occurs in the wandering larvae, which besides dying on the surface of the grain (Table 9) also die on walls, etc., and in crevices. The mortality of larvae which had left the grain was investigated by placing rolls of corrugated paper on the grain at various points in the room. These rolls were left on the grain for a week, by which time many

TABLE 8.

Weekly counts of larvae in 1943 and 1944 and the accumulated totals deduced from them.

Date of count, 1943	No. of larvae (nearest 100)	Date of count, 1944	No. of larvae (nearest 100)
19.viii.	[25]	17.viii.	[50]
26.viii.	1,500	24.viii.	1,000
2.ix.	54,400	31.viii.	28,800
9.ix.	87,500	7.ix.	190,400
16.ix.	87,100	14.ix.	257,900
23.ix.	49,400	21.ix.	178,500
29.ix.	32,200	28.ix.	107,800
7.x.	9,900	5.x.	54,800
14.x.	2,800	10.x.	39,800
21.x.	1,500	19.x.	18,400
28.x.	1,300	26.x.	10,300
4.xi.	600	2.xi.	5,700
11.xi.	1,300	9.xi.	3,200
18.xi.	300	16.xi.	2,500
Total observed	329,825	Total observed	899,150
Accumulated total	989,475	Accumulated total	6,165,600

larvae had entered them for hibernation. In 1943, the rolls were put into artificial crevices made by nailing boards to the ceiling with corks to separate them from it by half an inch. The rolls were then removed from the warehouse at intervals between 8.xi.43 and 1.viii.44 and the proportions of dead and living larvae recorded. The mortality discovered in this way may be due to any cause but is probably chiefly due to wilt. In 1944, the rolls were all taken

TABLE 9.

30 samples of grain taken on 9.xi. and 7.xii.44 to estimate numbers of dead larvae (figures for depths below 100.0 cm. based on 13 samples; figures for 25.0 cm. based on 60 samples, half of them large).

Depth	0	8.0	25.0	50.0	75.0	100.0	>100.0
Wt. of sample, g.	1468	2166	6393	1851	1813	1684	262
No. of dead larvae	148	85	120	1	0	0	0
Dead larvae per lb.	45.9	17.7	8.5	0.25	—	—	—

to Slough where they were kept in an unheated outhouse and examined between 27.x.44 and 5.iv.45. It was found in 1943 the mortality was increased in the samples examined later. The figures for 1943 suggest that there was a mortality of 58.2% in the first part of the winter probably entirely due to wilt. Later, in the period when larvae are beginning to awaken from diapause, there is a further mortality, making a total of 70%. The additional mortality of 11.8%

may or may not be due to wilt. In 1944 the mortality figures were erratic. It was found that when the rolls of paper were sorted out according to the part of the room where they had been exposed, there were wide differences both in the numbers of larvae per roll and in the percentage mortality. Some areas of the room had less than fifty per cent. mortality, whereas in others it was seventy per cent. or more. As the numbers of rolls were not proportional to the size of the various areas, or to the numbers of larvae in different areas, it was thought better to take an average of the percentages in different areas rather than to take a figure based on the total number of dead and living larvae in all

TABLE 10.
Mortality of larvae from "wilt" in 1943-44.

1943			1944		
Rolls exposed 29.ix. " retrieved 7.x.			Rolls exposed 14.ix. " retrieved 21.ix.		
Date examined	No. of larvae in sample	% dead	Date examined	No. of larvae in sample	% dead
8.xi.	330	58.2	9.x.	617	60.9
2.xii.	271		27.x.	1076	44.6
10.i.44	431		15.xii.	1550	70.5
10.ii.	631		21.i.45	2254	43.7
15.iii.	386	70.0	12.ii.	2050	79.6
11.iv.	414		21.iii.	916	61.5
5.v.	657		5.iv.	9428	57.5
6.vi.	459		Wooden crevices exposed 21.ix. " retrieved 7.xii.		
14.vi.	477				
1.viii.	222	65.3	15.i.45	1067	79.1
Pupal mortality (warehouse larvae kept at Slough)			Previous data arranged according to locality instead of date of examination		
May-Aug. 1944			84.7, 82.7, 79.1, 77.2, 77.0, 75.6, 74.2, 71.5, 71.4, 70.7, 69.4, 69.4, 69.1, 68.1, 68.0, 65.6, 58.6, 56.5, 51.2, 49.9, 43.1, 38.8, 23.0.		
No. pupating	No. emerging	% dead	Mean = 64.99, say 65.0%.		
253	230	9.1			

the rolls taken together. Together with the figures from rolls are included, in 1944, larvae obtained in some artificial wooden crevices nailed for 11 weeks on to a bulkhead.

A count was made of dead larvae of the 1943 generation found on 17 one-foot squares of grain (10.i.44) and on the usual areas of walls, pillars, ceilings, etc. (11.xi.43). These counts gave estimates of 437,800 dead larvae on the surface of the grain and 29,100 on walls, etc., making a total of 466,900. This partly corresponds to the mortality estimated from larvae in corrugated paper rolls but would be expected to be smaller since the latter includes that fraction of larvae which die after having entered crevices.

A figure is also available for pupal mortality in the spring of 1944 (*i.e.* ex 1943 larvae). Of 253 larvae pupating out of doors at Slough, 230 emerged, giving a pupal mortality of 9.1%. The data on "wilt" are shown in Table 10.

After allowing for all larval mortality, a figure is obtained for the number

of live hibernating larvae in crevices. An attempt was also made to estimate this number directly by pulling larvae out of a number of sample crevices with books made of bent wire. As was expected, only a fraction of the larvae present can be obtained in this way but there is some evidence that about the same fraction is found on each occasion. Thus, on 11.v.43, it was estimated that there were 12,300 larvae in crevices and later (Table 3) 59,700 moths were produced. Calling the factor by which the estimate must be multiplied x , then $12,300x \cdot \frac{89.4}{100} = 59,700$; $x = 5.4$ (89.4% is the proportion of pupae which produce moths).

TABLE 11.
Collected estimates of larval numbers, 1943-44.

No.	Estimate of—	Credit	Debit	Source of figures
1	1943, 1st stage larvae	3,645,450	—	Table 4.
2	Larvae dying in grain	—	2,655,950 = 72.9%	Not estimated, but obtained by subtracting 3 from 1.
3	Wandering larvae	989,500	—	Table 8.
4	Emerging as 2nd generation	—	1,000	p. 277.
5	Remaining larvae	988,500	—	Subtracting 4 from 3.
6	Deaths due to wilt	—	691,950 = 70%	Table 10.
7	Survivors in crevices	296,600	—	Subtracting 6 from 5.
8	Larvae found in crevices	99,800	—	p. 275.
9	1944, 1st stage larvae	12,809,200	—	Table 5.
10	Death of young larvae in grain	—	2,583,200 = 20.2%	Subtracting 12 + 13 from 9.
11	Surviving larvae	10,226,000	—	Adding 13 to 12.
12	Death of older larvae in grain	—	4,060,400 = 39.7%	p. 272.
13	Wandering larvae	6,165,600	—	Table 8.
14	Emerging as 2nd generation	—	4,500	p. 278.
15	Remaining larvae	6,161,100	—	Subtracting 14 from 13.
16	Deaths due to wilt	—	4,004,700 = 65%	Table 10.
17	Survivors in crevices	2,156,400	—	Subtracting 16 from 15.
18	Larvae found in crevices	291,900	—	p. 275.

Again, the number of larvae in crevices on 1.xii.43 was estimated as 99,800. The number of moths produced was 312,800. $x = 3.5$.

Similar figures are available for another room in 1943 and these give $x = 3.8$. In making a forecast of the numbers of moths to be expected in 1945, x has been taken as 4.0. The number of larvae found was 291,900.

A summary of the various estimates of larval numbers is made in Table 11. The following points in the table may be noted. (1) The two figures (1 and 9) given for numbers of 1st stage larvae are supported by those derived from the estimates of larval damage (p. 270), at least to the extent that they are of the right order. (2) The allowances for a small number of caterpillars producing second-generation moths in the autumn (4 and 14) are taken from pp. 277-278. (3) The greatest weakness in the budget is the absence of a direct determination

of the deaths of young larvae in the grain. The figures which were obtained by subtraction have been expressed as a percentage mortality in the two years. (4) The difference between the number of moths expected in 1944 and the number which actually emerged might be accounted for by an error in the determination of the wandering period of larvae. It can be calculated that to get the right number of moths 1,166,300 larvae would be required, and from the data in Table 8 this would mean a wandering period of 47.6 instead of 56 hours. The figure of 56 hours is certainly not very reliable since weekly counts were too infrequent. (5) As explained on p. 275, the number of larvae actually found in crevices is always too low and must be multiplied by a factor x (lying between 3.5 and 5.5) to get the estimate of moths expected in the following year.

7. PARASITES AND PREDATORS.

Insect parasites of the larvae were very rare. A few examples of *Nemeritis canescens* (Gravenhorst) and of *Angitia chrysosticta* (Gravenhorst) (two bred) (ICHNEUMONIDAE) have been observed. The percentage attack must have been below 0.1%. In 1944, a small number of *Microbracon hebetor* (Say) (BRACONIDAE) were bred from warehouse larvae in corrugated paper rolls, but the percentage attack, though not accurately determined, was certainly very low.

In the autumn of 1944 the spider *Tegenaria domestica* (L.) (det. W. S. Bristowe) became common in the room and a number of moths were caught in the webs. On 26.x. an estimate of spiders numbers on 77 sample areas gave a total for the whole room of 585 (all immature; some were later reared to maturity). On this date the webs of 101 spiders contained 131 moths of which 115 were male. At this date (see p. 285) the sex ratio of moths was about 2 ♀ to 9 ♂, but even so there was an excess of males in the webs. This may be due to the greater activity of males or to the attraction exercised by any females which happen to get caught. A similar excess of males was noted in 1943 amongst moths caught on fly-papers although the true sex-ratio was 2 ♂ : 3 ♀.

On 26.x., all webs were removed from the sample areas which were re-examined on 9.xi. On that date there were 20 spiders on these areas and 44 dead moths in their webs. The rate of predation was therefore about 2 moths per spider per fortnight.

On 28.x.1944, mites, *Typhlodromus tineivorus* Oudemans (= *Seiulus muricatus* of authors) (GAMASIDAE) (det. M. E. Solomon), were noticed hanging on to moths. This mite is known to be predatory on the early stages of various insects. In the case of *E. elutella*, the eggs are eaten, the wings of the moths may be crippled by being attacked before expansion, or if attacked later the wings may be outspread instead of folded over the back. Collections of moths to estimate the importance of this mite were made between 28.x. and 22.xi. with results shown in Table 12. If the mites occurred earlier in the year and the same percentage of moths was attacked, the effect would be important. Burkhardt (1919) recorded that this mite feeds on the eggs of *Ephestia kühniella* Zeller, and Livingstone and Reed (1936 : 1019) and Bare (1942 : 188) record "*Seiulus* sp." attacking *E. elutella*.

Mice and rats occur in the room and at least the former are known to eat *Ephestia* larvae and pupae. It is not known whether their activity has any importance in this respect in the granary.

TABLE 12.

Incidence of the mite *Typhlodromus tineivorus* Oudemans in the autumn 1944.

Date	♂				♀			
	No. collected	No. with mites	%	No. of mites per moth with mites	No. collected	No. with mites	%	No. of mites per moth with mites
19.x.	—	—	—	—	15	8	53	—
26.x.	76	40	52.6	1-23, av. 4.0	7	7	100	One with 13, others not counted
2.xi.	73	30	41.1	1-5, av. 2.4	10	10	100	1-5, av. 3.5
9.xi.	32	4	12.5	1-2, av. 1.5	10	5	—	—
16.xi.	30	1	—	1 with 1 mite, 8 with crippled wings	—	—	—	—
22.xi.	14	3	—	4 mites (total), 6 with crippled wings	12	3	—	1, 1, 2 mites, 5 with crippled wings

8. SECOND GENERATION OF MOTHS.

Although the two generations overlap, it was found in 1944 by Mrs. M. J. Richards' dissections that a line between them could be drawn by counting the number of spermatophores per female and by counting the number which had paired once or not at all. These two figures on 7.ix. were 3.7 and 0 and on 14.ix. were 1.7 and 50% (fig. 3). Therefore 7.ix. is taken as the end of the first generation. In 1943, moths were not dissected, but on the basis of moth counts, the first generation ended about 2.ix. Table 13 gives the moth counts of the second generation.

In 1943, the longevity of 63 ♀, 66 ♂ was determined (as described in Appendix 1) and was 37 days ♀, 26 days ♂; the length of life increased after Sept. when the temperature began to fall. By inspection, it is concluded that the second generation consisted of about 1000 moths. Of 170 moths caught, 79 were ♀, giving a sex ratio of 8 ♀: 9 ♂. Therefore in the 1000 moths there would be 470 ♀. Their fecundity determined from 63 ♀ in the warehouse was 79, so that

TABLE 13.

Moth counts for the 2nd generation, 1943-44.

Date, 1943	No. of moths	Date, 1944	No. of moths
2.ix.	70	7.ix.	70
9.ix.	20	14.ix.	90
16.ix.	90	21.ix.	30
23.ix.	80	28.ix.	240
29.ix.	200	5.x.	770
7.x.	760	10.x.	1570
14.x.	590	19.x.	3120
21.x.	160	26.x.	3950
28.x.	270	2.xi.	1550
4.xi.	120	9.xi.	500
11.xi.	180	16.xi.	200
18.xi.	0	22.xi.	200
24.xi.	0	7.xii.	110

about 37.130 eggs may have been laid. On 10.i.1944, 17 samples of about 360 g. were taken but only one pupa and two 6th stage larvae, which might have belonged to the first generation, were found. Eggs from warehouse moths laid in September–October 1943 were kept in jars of grain in an unheated outhouse at Slough and produced larvae which fed and developed slowly throughout the winter. They produced moths rather later in 1944 than those from first-generation larvae. As the grain was removed in February 1944, the second-generation larvae cannot have contributed materially to the 1944 population.

In 1944, the second generation probably consisted of 4000–5000 moths. The sex-ratio in September was not very far from 1 ♂ : 1 ♀ but in October and November it was 5 ♂ : 1 ♀ (723 ♂ : 147 ♀, see p. 285). There were probably about 100 ♀ in September and 670 ♀ later. At 25° C., 40 of these females had a fecundity of 46, so there may have been about 35,600 eggs produced. A sample of about 5.82 kg. was taken on 7.xii.44 and contained two 6th and one

TABLE 14.

Emergence-rate of moths from eggs and larvae kept in an unheated outhouse at Slough.

Date of eggs laid or larvae collected	No. of larvae	No. dying	Emergence dates							
			1943		1944					
			ix.	x.	5–18.vi.	19.vi.–2.vii.	3–16.vii.	17–30.vii.	31.vii.–13.viii.	14–28.viii.
Eggs laid (in warehouse), 1.vi.43	Not recorded	Not recorded	8	1	0	37	8	0	0	0
Eggs laid (in warehouse), 1.vii.43	"	"	2	1	0	30	43	1	0	0
Eggs laid (in warehouse), 3.viii.43	"	"	0	0	0	0	34	21	9	0
Larvae collected: 2.ix., 7.x.43	"	"	0	0	0	0	34	21	9	0
16.ix.43	97	40	0	0	8	28	19	1	1	0
23, 29.ix., 7.x.43	280	160	0	0	4	43	45	25	2	1
14, 21, 28.x.43	180	131	0	0	0	12	14	17	5	1
4, 11.xi.43	48	44	0	0	0	0	3	0	1	0

5th stage larva, which might have belonged to the first generation. In the low temperatures prevailing in November, the moths seemed hardly able to move or pair. Out of 31 ♀, 24 were virgin.

The probable source of the small second generation is referred to in the next section.

9. DIAPAUSE IN FULLY FED LARVAE.

The reasons why wandering larvae undergo a prolonged resting period before pupation are very imperfectly understood, but some reference must be made to the subject since it is the entry into diapause which ensures that for most of the moths there is only one generation a year in this country.⁴

Larvae from the granary or from eggs laid by granary moths mostly have a diapause even when kept at 25° C. Tables 14 and 15 show the emergence of (a) larvae from eggs laid by warehouse moths and of warehouse larvae, both kept at Slough in an unheated outhouse, (b) of warehouse larvae put at 25° C. in the autumn, one day after collection, (c) of larvae from eggs laid by ware-

⁴ In other countries there may be more than one generation in a year. Reed and Livingstone (1937) record three generations on tobacco at Richmond, Virginia. The temperatures are mostly 21–27° C. instead of 15–20° C., as found in the London granary. It is not known what effect tobacco as a food has on the larval diapause. Potter (1935) speaks of the two annual generations of *E. elutella* in this country on dried fruit.

house moths, kept throughout at 25° C., and (d) of warehouse larvae put at 25° C. in February, after being kept in warehouse or outhouse conditions until that date.

The figures in Table 14 show that the second generation of moths must be derived almost entirely from eggs laid at the beginning of emergence by early moths. Also, the earlier collected larvae produce earlier moths in the following year. These differences may be partly genetic but since (Table 17) early larvae

TABLE 15.

Pupation-rate of larvae from eggs laid at 25° C. 70% R.H., or of larvae placed in those conditions on different dates.

Date eggs laid, or larvae put at 25° C.	No. of larvae	No. dying	Months at 25° C.							
			1	2	3-4	5-6	7-8	9-10	11-12	13-14
Eggs laid 16.iii.44 (ex larvae 10.ii.44)	40	11	0	0	3	7	5	13 ¹	0	0
Eggs laid 6-27.x.44 (ex larvae ix.44)	213	56	9	2	4	2 ²	0	0	0	0
16.ix.-11.xi.43 (25° C. at one day after collection)	1040	815	77	54	12	21	19	26	14	1 ³
30.i.45 (25° C. at one day after collection)	100	9	91 ⁴	0	0	0	0	0	0	0
3.iii.45 (25° C. at one day after collection)	40	14	26	0	0	0	0	0	0	0

¹ One still in diapause at 13 months. ² 140 still in diapause at 5 months. ³ One larva lost.
⁴ 118 larvae of same generation put at 25° C. on 11.xi.44, 69.5% still in diapause after 5 months.

are heavier and weight of fully fed larvae is related to diapause, the effects of crowding or of nutritional factors may also be involved.

The figures in Table 15 give pupation-rates at 25° C.; at this temperature emergence takes place 14 days later, with little variation. The pupation rate at a constant temperature still clearly shows the effect of diapause, though pupation is spread out over a much longer period than in larvae exposed to the

TABLE 16.

Pupation of larvae in corrugated paper rolls kept in the warehouse, winter 1943-44.

Date roll examined	1943		1944						
	4.xi.	1.xii.	10.i.	10.ii.	15.iii.	11.iv.	5.v.	6.vi.	14.vi.
No. of live larvae .	154	160	166	257	100	146	188	57	36
No. of pupae .	4	2	0	6 ¹	16	1	3	74	114
% .	2.5	1.3	0	2.3	13.8	0.7	1.6	56.4	81.4

¹ One of these had already emerged.

normal climatic cycle. On the other hand, larvae collected in the New Year, possibly because they have experienced low temperatures (minimum in January -8° C.), pupate within two weeks when placed at 25° C. In unheated conditions, larvae after January pupate slowly, a few each month, the process not becoming rapid until late May. Emergence automatically follows pupation, after an interval depending on the temperature. This is shown in Table 16,

which gives the number of pupae amongst the larvae in corrugated paper rolls in the warehouse 1943-44. About 5 days before pupation at 16° C. (1 day at 25° C.) the ocellar pigment of the larvae is retracted. The stages of this process have been studied and they do not differ materially from those of *E. kühnella* Zeller, described by Kühn and Piepho (1936).

Larvae in diapause are not necessarily completely inactive. Small quantities of faeces may be passed at intervals during diapause and more again just before pupation. Very occasionally larvae apparently already in the sixth instar may moult during diapause. Two out of 253 did so in larvae kept in an unheated outhouse and three out of 225 of those kept at 25° C. Of the 5 larvae with the extra moult, 2 died and 3 pupated about a month after the moult. In early May, a small number of hibernated larvae wander slowly about on ceilings, etc., in the warehouse. About 100 such larvae were visible in the warehouse room on 5.v.44. Of 257 larvae which were hibernated in tins at

TABLE 17.

Weights of wandering larvae collected in the warehouse on successive dates in 1943 and 1944, with percentage survival and original weights of survivors and non-survivors.

Date collected, 1943	16.ix.	23.ix.	29.ix.	7.x.	14.x.	21.x.	28.x.	4.xi.	11.xi.
No. weighed (singly)	70	79	97	84	75	53	36	32	16
Mean wt., mg.	17.8	16.1	17.2	16.1	12.8	10.7	10.5	10.0	12.0
% survival	63	58	29	50	23	21	19	9	6
Original wt. of survivors	18.3	17.0	18.3	17.2	15.3	13.6	13.4	16.3	15.0
Original wt. of non-survivors	17.0	14.8	16.4	14.9	11.6	9.8	9.9	9.3	12.0
Date collected, 1944	31.viii.	7.ix.	14.ix.	21.ix.	21-27.x.	3.xi.	22.xi.	8.xii.	
No. weighed (singly or in groups)	213	100	100	200	370	325	200	225	
Mean wt., mg.	14.9	16.0	13.9	11.7	10.6	10.1	11.6	10.3	

¹ Certain abnormally small larvae (discussed later) have been omitted.

Slough, 17 wandered for a time in May and June, in some cases leaving their cocoons to do so.

Larvae which start wandering early in the autumn are heavier than those which wander later and this appears to be related both to subsequent mortality and to diapause. The figures in Table 17 show (a) that successive batches of larvae in the autumn tend to be lighter in weight, (b) that more of the later batches die, (c) that the survivors tend to have a higher and the non-survivors a lower weight on the date of collection. As a result of (b) and (c), the average weight of a population of warehouse larvae may appear to go up during the winter, although the individual larvae can be shown to lose weight as a result of metabolism; this apparent increase is of course due to the gradual elimination of all the larvae which were very light at the date of collection. These data are also shown graphically in fig. 7, where it can be seen that mortality is much greater amongst lighter larvae and is much the heaviest in the autumn.

If the surviving larvae from Table 17 are grouped according to weight, irrespective of date of collection, a relation can be seen between larval weight and the time which elapses before pupation. This is shown in Table 18 and in fig. 8 for warehouse larvae kept in an outhouse at Slough. The effect of larval weight on length of diapause is greater than that of date of collection. The correlation coefficient between length of diapause and larval weight = + 0.3885

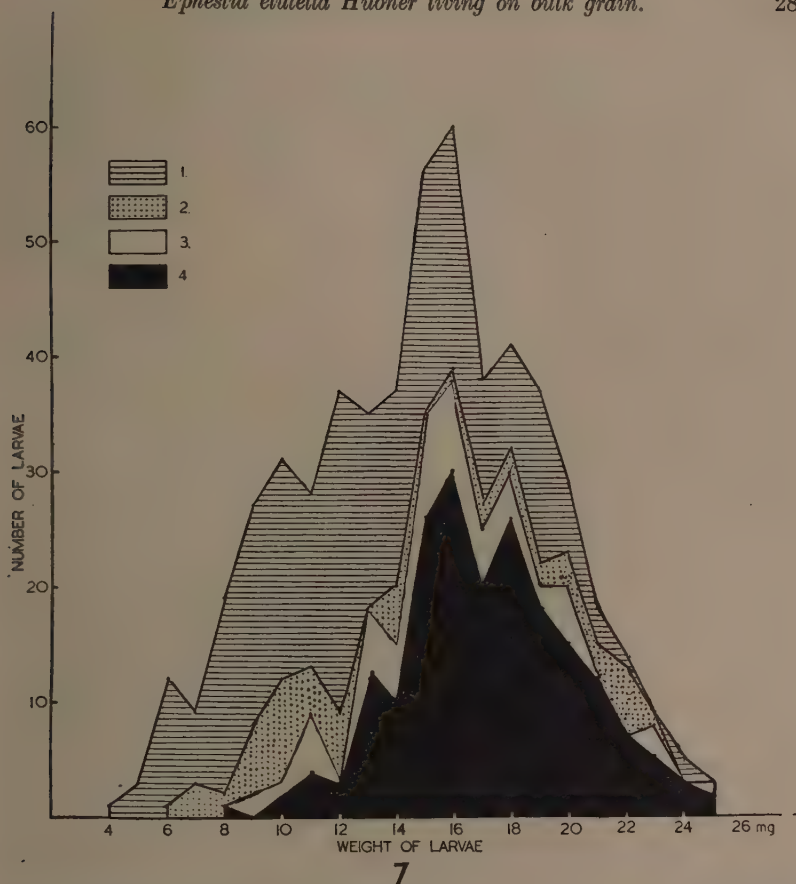


FIG. 7.—Weight frequencies of larvae (weighed on day of collection), (1) on date of collection (Sept.-Nov. 1943); (2) original weights of those surviving to Jan. 1944; (3) original weights of those surviving to March 1944; (4) original weights of all those producing moths in June-Aug. 1944.

TABLE 18.

Length of diapause in warehouse larvae kept in an outhouse at Slough, arranged according to original weight of larvae.

Diapause = number of days from date of collection to date of pupation. Only pupae which produced moths are included.

Weight of larvae, mg.		No. of larvae	Length of diapause, days	
Range	Mean		Range	Mean
21.5-25.0	22.96	16	229-268	254.0
17.0-21.0	18.72	88	210-305	244.2
12.5-16.5	14.93	82	190-260	235.9
8.0-12.0	10.75	10	205-240	225.6

($P = <0.01$); between length of diapause and date of collection = -0.3597
($n = 194$)
($P = <0.01$); between length of diapause and larval weight, eliminating the
effect of date of collection, the partial correlation coefficient = $+0.3114$
($P = <0.01$).
($n = 193$)

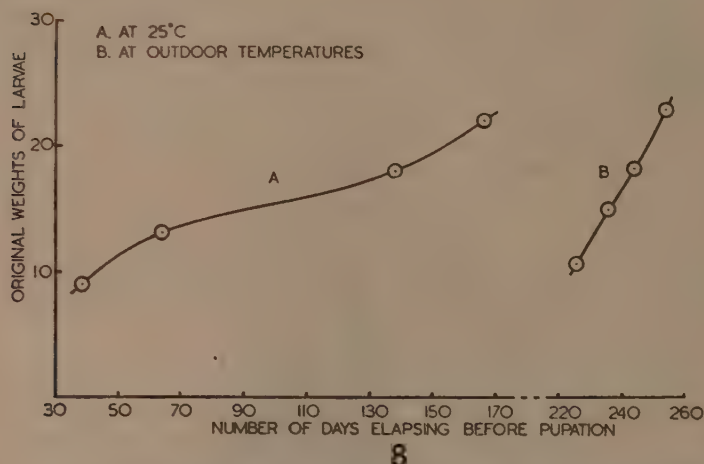


FIG. 8.—Curves relating original weights (grouped) of larvae to time elapsing before pupation at 25° C. and at outdoor temperatures.

A parallel effect of weight on the length of diapause can be seen in samples of the same larval populations kept at 25° C. 70% R.H., though the periods are shorter on the average. The data are shown in Table 19 and fig. 8. The results seem to be quite independent of date of collection. Amongst the

TABLE 19.

Length of diapause of warehouse larvae kept at 25° C., 70% R.H., arranged according to original weight of larvae.

Weight of larvae, mg.		No. of larvae	Length of diapause, days	
Range	Mean		Range	Mean
Instar VI.				
20.5-25.0	22.14	21	22-361	166.5
16.0-20.0	18.05	66	16-323	138.2
10.5-15.5	13.27	89	9-306	64.2
5.5-10.0	9.02	31	1-269	38.8
Instar V				
20.5	20.5	1	—	108
16-20	17.3	6	19-261	175.7
10.5-15.5	13.2	26	9-306	72.7
5.5-10.0	8.9	17	1- 35	21.2

larvae collected in the warehouse were some small ones which were thought to be of the type having five instead of six instars. All these were kept at 25° C. and this is why there are more small larvae in Table 19 than in Table 18. However, as far as the relation between weight and length of diapause goes, the supposed fifth instar larvae behaved just like the others, so they have been included with them in Table 19. In fig. 8 it can be seen that the curve relating weight to length of diapause at 25° C. is somewhat S-shaped, as might perhaps be expected. The straight-line relation in larvae kept out of doors is more surprising.

These data about diapause can be summarised as follows :—

(1) Nearly all larvae have a diapause, the few non-diapausing larvae which produce the second generation of moths developing from eggs laid by the earliest emerging moths of the first generation. Such moths may belong to a genetic stock, part of the offspring of which form the second generation in each year.

(2) Warehouse larvae collected in the autumn and early winter do not easily end their diapause by pupation, even at 25° C. At this temperature pupation is spread over a very long period, up to 300 days.

(3) Warehouse larvae collected in Jan. or later, all pupate in 2-3 weeks when put at 25° C. This may be because they have experienced low temperatures.

(4) The earlier wandering larvae tend to be heavier than the later ones. Irrespective of the date of wandering, heavier larvae are more likely to survive to pupation.

(5) There is a longer interval before pupation in heavy larvae than in lighter ones, both at outdoor temperatures and at 25° C. At outdoor temperatures, however, the light larvae, though having a shorter diapause, produce moths later in the following year because they wander later than the heavy ones, i.e. there is a greater range in the date of wandering than there is in length of diapause.

10. EFFECTS OF CROWDING.

It can be shown in laboratory cultures that *Ephestia* larvae bred under crowded conditions have a high mortality and tend to be small. The effect of crowding on mortality is shown in Table 20.

TABLE 20.

Effect of crowding on mortality of larvae (insectary stock). Cultures of 200 g. at 25° C., 70% R.H. Area of surface 34.2 cm.²; depth 9 cm.

Original no. of larvae	25	50	100	150	200
No. of replicates	7	6	6	2	5
Surviving no. of larvae	22, 22, 22, 20, 24, 16, 10	31, 45, 35, 30, 30, 37	51, 94, 85, 42, 68, 64	75, 69	103, 72, 113, 101, 135
Average mortality, %	22.4	30.8	32.7	52.0	47.6
Grains per larva (approx.)	276	138	69	45	34
Larvae per sq. foot	676	1351	2702	4053	5404

It seems surprising at first sight that larvae with 138 grains available should exhibit the effects of crowding when only about 50 grains (p. 270) are really needed. But it seems clear that the surface area of the grain is more important than the volume. Larvae reared singly under similar conditions

seem to show even less mortality, *e.g.* 1 larva on 150 grains, 65 out of 75 survived; 1 larva on 350 g., 80 out of 80 survived for 2-3 weeks; 2 larvae on 250 g., 30 out of 40 survived to 2 weeks.

The data relating larval weight to degree of crowding are not altogether reliable as there seems to have been some mortality due to "wilt." On these grounds we have rejected five cultures; apparently those infected by wilt usually produce very small larvae. The data from the other cultures are given in Table 21. These figures show a relation between crowding and the weight

TABLE 21.

Survival to wandering and weights of larvae bred on 70 g. wheat at 25° C., 70% R.H.
Area of surface 19.6 cm.²; depth 6.5 cm.

Initial no. of larvae	% survival (to wandering)	Average weight of surviving larvae, mg.	Larvae per sq. ft. of grain surface
7	100	21.3	330
10	50	22.2	472
10	50	21.0	472
15	55.5	17.1	707
25	40.0	12.8	1178
25	56.0	15.2	1178
30	60.0	18.0	1415
33	69.6	14.4	1556
35	82.8	16.8	1650
35	48.6	19.5	1650
35	25.5	15.0	1650
40	77.8	11.3	1886
70	28.6	10.9	3300
75	42.7	8.9	3536
80	67.5	8.9	3772
100	49.0	15.1	4715

of the resulting larvae; the irregularities are at least partly due to variations in mortality.

The density of larvae in Tables 20 and 21 has also been expressed in terms of larvae per square foot of surface so as to be able to compare the results with oviposition observed in the warehouse. Since most of the larvae keep near the surface the much greater depth available in bulk grain does not make as much difference as might be expected. On the other hand, instead of larvae of the first instar being added to the grain on one day (as in a jar), eggs are added to the grain surface over a period of more than seven weeks. Crowding is progressive and is more intense for the later larvae which will find many grains already lacking embryos. A rough and minimum estimate of the crowding effect can be obtained by noting the oviposition per square foot obtained from "tray" data.

Larvae per sq. ft.	Tray most laid on	Tray least laid on
24.vi.-8.vii.1943	345	63
6.vii.-19.vii.1944	1670	312

Examining the weights of larvae in 1943 and 1944, given in Table 17, it is clear that so far as they are influenced by crowding, this must be due to the cumulative effect of seven weeks' oviposition. Even in the most crowded tray, the number of larvae per square foot does not compare with the number

in the more crowded cultures. It is possible, also, that sublethal infection by "wilt" reduces the weight of warehouse larvae. In the autumn of 1944, when larvae started wandering, it was noticed that some very small larvae were leaving the grain, particularly in certain spots. Some of these larvae were kept in the laboratory in tubes with grain, but only about 10% of them did any further feeding. The remainder either died, pupated or entered diapause. Later in

TABLE 22.

Weight distribution of wandering larvae. Nos. of larvae of wt. classes.

Weight class, mg.	31.viii.44	14.ix.44
20 -24	8	4
17 -19	26	12
14 -16	29	35
11 -13	27	28
8 -10	10	19
5 - 7	0	2
		} Random collection of 100 larvae.
8 -10	8	
5.5- 7.5	7	
3.5- 5.0	10	
2.5	0	2
		} Set of larvae picked out as small in the warehouse.

the season, as the average size of larvae decreased, small larvae were not so evidently different from the general population. The following weight distributions (Table 22) show that early in the wandering period the small larvae form a separate group. They formed about 9% of the population on 31.viii. and about 0.4% on 14.ix. It is probable that such larvae are in some way produced by crowding.

TABLE 23.

Sex-ratio of *E. elutella* in the warehouse.

		♂	♀	Total	♂ : ♀
1st gen. 1942 (not the room studied in 1943-44)	Dead moths	217	337	554	2 : 3
1st " 1943	Live "	398	610	1008	2 : 3
2nd " 1943	" "	91	79	170	9 : 8
1st " 1944	Dead "	850	854	1704	1 : 1
2nd " 1944 Sept.	Live "	—	—	about	1 : 1
5.x.-19.x.	" "	394	85	479	4.6 : 1
26.x.-2.xi.	" "	254	26	280	9.8 : 1
9.xi.-22.xi.	" "	75	36	111	2.1 : 1

There is no experimental evidence that crowding affects the sex-ratio in *Ephestia* but such an effect has been recorded in other insects, e.g., *Lymantria monacha* L. (Brandt, 1938), *Archips fumiferana* Clemens (Graham, 1939), *Lucilia sericata* Meigen (Herms, 1928), *Trichogramma evanescens* Westwood (Salt, 1936).

Such effects might be produced either by differential mortality (Goldschmidt, 1923 : 233) or by an alteration of sex due to starvation (Holdaway and Smith, 1932, 1933).

The following records of sex-ratio were obtained in the warehouse (Table 23).

There seems to be an indication here that more males are produced when larvae develop under crowded conditions. The low proportion of males in 1942 and 1943 may be partly due to males flying out of the windows more often than females. The reduction of the proportion of males in November 1944 is probably more apparent than real, since the females live longer and tend to predominate at the end of a generation.

It is perhaps more likely that if crowding does affect the sex-ratio this should be through differential mortality rather than through starvation. For in *E. elutella*, it takes a heavier caterpillar to produce a male than a female moth of the same weight (Table 24). It would not therefore be expected that starvation would produce more males.

TABLE 24.

Relation between weight of larva and weight of moth produced (reared in unheated outhouse).

Range in wt., mg.	♂♂			♀♀		
	No. of larvae	Mean wt., mg.	Mean wt. of moths	No. of larvae	Mean wt. mg.	Mean wt. of moths
20.5-25.0	12	21.5	7.7	12	22.1	9.3
16.5-20.0	43	18.2	6.7	27	17.8	8.0
12.5-16.0	35	15.0	5.9	25	14.6	7.0
8.5-12.0	4	11.4	5.4	4	10.8	6.3
—	—	—	—	1	8.0	5.5

It may be noted that if crowding does produce small larvae, such larvae will produce small moths. These moths will lay fewer eggs (see Appendix 3, p. 295 and fig. 11). The small larvae will also tend to have a shorter diapause (Table 18). It is possible that the reduction in weight of wandering larvae as the autumn progresses (Table 17) may be produced by progressive crowding of larvae in the grain. When adults are sufficiently numerous they are more active, even in the daytime, apparently through mutual stimulation. Having developed under crowded conditions, the moths will already be small, and this, together with the greater activity, will result in reduced length of life and fecundity (compare figures for 1943 and 1944, pp. 295-296).

11. DISCUSSION OF RESULTS.

The results of this study can be mostly conveniently summarised in a series of credit and debit estimates, shown in Table 25 and also fig. 9. The least satisfactory estimates are those of hibernating larvae in crevices (one-sixth-one-third of true number found) and of young larvae dying during the feeding stage (not directly estimated). The only vital discrepancy is between figures 10 and 11, about 16.1% more moths emerging than were expected. Where, as in the numbers of moths in 1944 (figures 11, 11a and 11b), there are independent estimates of one variable, the estimates vary by about the same amount (8.8-14.3%). The discrepancy between 21 and 23 is discussed in Appendix 4.

On p. 261, it is suggested that the ratio between the number of moths which emerge in one generation and the greatest number seen in the room on one day is about 1.6 and this figure may have a certain practical application.

TABLE 25.

No.	Estimate of—	Credit		Debit	Source of figures
		Primary estimate	Supplementary estimates		
	1943				
1	Larvae in crevices	12,300	—	$x = 5.4$	p. 275.
2	Moths, 1st gen.	59,700	—	—	Table 3.
3	Eggs	4,050,500	—	—	Table 4, D.
3a	"	—	4,439,200	—	Table 4, E.
4	Infertility of eggs	—	—	405,050 = 10%	Table 4.
5	1st stage larvae	3,645,450	—	—	Subtracting 4 from 3.
6	Wandering larvae	989,500	—	72.9% died in grain	Table 11.
7	Death due to wilt and emergence of 2nd gen.	—	—	692,950 = 70.00%	Table 11.
8	Larvae in crevices	296,600	—	—	Subtracting 7 from 6.
8a	"	—	99,800	$x = 3.5$	p. 275.
9	Pupal mortality	—	—	27,000 = 9.1%	Table 11.
10	Moths expected 1944	269,500	—	—	Subtracting 9 from 8.
	1944				
11	Moths, 1st gen.	312,800	—	—	Table 3, A.
11a	"	—	357,600	—	Table 3, C.
11b	"	—	285,200	—	Table 3, D.
12	Eggs	14,232,400	—	—	Table 5.
12a	"	—	13,294,000	—	p. 267.
13	Infertility of eggs	—	—	1,423,200 = 10%	Table 5.
14	1st stage larvae	12,809,200	—	—	Subtracting 13 from 12.
14a	"	—	11,964,600	—	Using estimate 12a.
15	Young larvae dying in grain	—	—	2,583,200 = 20.2%	Subtracting 16 + 17 from 14.
15a	"	—	—	1,738,600 = 14.5%	Subtracting 16 + 17 from 14a.
16	Older larvae dying in grain	—	—	4,060,400	Table 11.
17	Wandering larvae	6,165,600	—	—	Table 11.
18	Deaths due to wilt and emergence of 2nd gen.	—	—	4,009,200 = 65.03%	Table 11.
19	Larvae in crevices	2,156,400	—	—	Subtracting 18 from 17.
19a	"	—	291,900	—	p. 275.
20	Pupal mortality	—	—	196,200 = 9.1%	Table 11.
	1945				
21	Moths expected	1,960,200	—	—	Subtracting 20 from 19.
22	"	—	1,167,600	$x = 4.0$	p. 275.
23	Moths found	277,800	—	—	Appendix 4.

In this specialised environment, physical conditions do not vary enough to be a major influence on the trend of the population. The most important effect of variations in temperature is on diapausing larvae the date of pupation of which is determined by (a) the cold weather of the winter and (b) the rising temperature of the spring. It is also possible that the lowness of British summer temperatures prevents more than a small fraction of the larvae emerging as a second generation.

The chief factor controlling the size of the population is the disease, probably bacterial, referred to as wilt. This destroys about 90% of all larvae. No clear evidence was found that the amount of larval mortality depended on the density of the population, which is therefore still increasing.

There is some evidence that the population has passed the optimum density for the species. In 1944, the moths were smaller than in 1943 and the size of the wandering larvae in 1944 suggests that in 1945 the moths will be still smaller. The reduction in size is accompanied by reductions in longevity (22.0 days 1943, 12.5 days 1944) and fecundity (124 eggs 1943, 91 eggs 1944), but it is not yet certain whether this can be pushed far enough to stop population-increase.

The steady increase in the *Ephestia* population of the room studied was in marked contrast to the stable or falling populations of other rooms in which control measures (spraying, sticky-banding) were applied and showed that even imperfect methods were more effective than might be supposed. The actual loss of grain on the floor studied was estimated at 973 lb. in 1943 and 2028 lb. in 1944 (out of about 500 tons) but this loss was nearly all of the valuable wheat-germ.

12. ACKNOWLEDGEMENTS.

Work in the granary was started in 1941-42 by T. A. Oxley of the Pest Infestation Laboratory, Dept. of Scientific and Industrial Research, and O. W. Richards.

N. Waloff, as a research assistant of Professor H. G. Jackson of Birkbeck College, has been working on *Ephestia* since January 1942, at first with a grant from the Royal Society, but later (1943-45) under the auspices of the Department of Scientific and Industrial Research.

From the beginning, Professor J. W. Munro has put the facilities of the Department of Zoology of the Imperial College of Science and Technology freely at N. Waloff's disposal, and since 1943 the work has become, in effect, a joint enterprise of the Department of Scientific and Industrial Research and the Imperial College.

The room at the granary and the wheat which it contained were provided by the Ministry of Food through the kind co-operation of Mr. W. McAuley Gracie. Much help in the detailed arrangements was given by Dr. J. A. Freeman, of the Ministry of Food. Our thanks are also due to many members of the Pest Infestation Laboratory staff who have helped in various ways.

13. SUMMARY.

1. The data on population changes in the moth *Ephestia chutella* Hübner are summarised in Section 11, and in Table 25 and fig. 9. The other main results are collected below.

2. Several methods for estimating the numbers of moths, eggs and caterpillars, the longevity of adults, and the length of the wandering stage in fully fed larvae have been devised and tested.

3. In appendices 1 and 3, respectively, it is shown that moths which are heavier on emergence live longer and lay more eggs.

4. It is shown that by dissecting samples of female moths, the changing age-distribution of the population can be detected, especially by the percentage of moths in which the fat-body is exhausted and in the average number of spermatophores per female bursa copulatrix. Such dissections also enable a line to be drawn between two overlapping generations.

5. It is shown that on the average in the course of development one larva eats 47.71 ± 1.04 embryos of Manitoba wheat and that this figure can be used to give a rough estimate of larval numbers.

6. Hymenopterous and Arachnid parasites and predators caused a negligible mortality of larvae and adults. Much the most important cause of death was a disease of the larvae, referred to as wilt, probably of bacterial origin.

7. In both 1943 and 1944, a few of the earlier maturing larvae pupated in the autumn and produced a small second generation of moths. Their number was only one-sixtieth to one-seventieth of that emerging in the first generation.

8. It is shown that successive batches of wandering larvae in the autumn tend to be lighter in weight; that lighter larvae have a higher mortality than heavier ones. As a result of this differential mortality, the average weight of groups of hibernating larvae may appear to rise, though each individual is really losing weight.

9. The earlier maturing larvae produce either moths of the second generation or those which appear earlier in the following year. As stated in (8), these early larvae are heavier than later ones; yet it is found that heavier larvae tend to have a longer prepupation period than lighter ones. This is possible because the period over which wandering larvae may be found is longer than that in which the majority of moths emerge in the following year.

10. Before Christmas, the temperature of 25°C . only gradually breaks the diapause of the larvae. After January, perhaps because they have experienced low temperatures, larvae placed at 25°C . pupate in a fortnight.

11. It was shown in laboratory experiments that in crowded cultures the mortality of larvae is increased and their weight reduced. Apparently similar effects, at least on weight, were observed under warehouse conditions. No close comparison, however, should be drawn between culture jars in which the larvae all start at the same age, and a large bulk of wheat to the surface of which eggs are added over a two-month period.

12. During the two years of study there appeared to be an irregular but progressive increase in the proportion of male to female moths. This may be due to a differential mortality in the larval stage.

14. REFERENCES.

- BARE, C. O., 1942, Some natural enemies of stored tobacco insects, with biological notes. *J. econ. Ent.* **35** : 185-9.
- BRANDT, H., 1938, Untersuchungen über die Änderung des Geschlechtsverhältnisses bei der Nonne (*Lymantria monacha* L.) und ihre Ursachen. *Z. angew. Ent.* **24** : 87-94, 2 figs., 2 tables.
- BURKHARDT, F., 1919, Zur Biologie der Mehlmotte (*Ephestia kühniella* Zell.). *Z. angew. Ent.* **6** (1919-20) : 25-60, 13 figs.
- DENDY, A., and ELKINGTON, H. D., 1919, On the phenomenon known as "webbing" in stored grain. *Rep. Grain Pests Comm. Roy. Soc.* **4** : 14-17.
- GRAHAM, S. A., 1939, Forest Insect Populations. *Ecol. Monogr.* **9** : 301-10.

- HERMS, W. B., 1928, The effect of different quantities of food during the larval period, on the sex ratio and size of *Lucilia sericata* Meigen and *Theobaldia incidens* Thom. *J. econ. Ent.* **21**: 720.
- HOLDAWAY, F. G., and SMITH, H. F., 1932, A relation between size of host puparia and sex ratio of *Alysia manducator* Panzer. *Aust. J. exp. Biol. med. Sci.* **10**: 247-59.
- , —, 1932, Alteration of sex ratio in the "Flour beetle" *Tribolium confusum* Duval, following starvation of newly hatched larvae. *Aust. J. exp. Biol. med. Sci.* **11**: 35-43, 1 fig., 5 tables.
- GOLDSCHMIDT, R., 1923, *The mechanism and physiology of sex determination* (trans. W. J. Dakin). London.
- KÜHN, A., and PIEPHO, H., 1936, Über die hormonalen Wirkungen bei der Verpuppung der Schmetterlinge. *Nachr. Geo. Wiss. Göttingen* [N.S.] **2**: 141.
- LIVINGSTONE, E. M., and REED, W. D., 1936, Insect fauna of cured tobacco in storage in United States. - *J. econ. Ent.* **29**: 1017-22.
- MUNRO, J. W., 1940, Report on a survey of the Infestation of Grain by insects. D.S.I.R. London, His Majesty's Stationery Office.
- NORRIS, M. J., 1933, Contributions towards the study of insect fertility. II. Experiments on the factors influencing fertility in *Ephestia kühniella* Z. (Lepidoptera, PHYCITIDAE). *Proc. zool. Soc. Lond.* **1933**: 903-34.
- , 1934, Contributions towards the study of insect fertility. III. Adult nutrition, fecundity and longevity in the genus *Ephestia* (Lepidoptera, PHYCITIDAE). *Proc. zool. Soc. Lond.* **1934**: 334-60.
- OXLEY, T. A., and HENDERSON F. Y., 1944, The properties of grain in bulk. I. Instruments for making measurements in grain stored in bulk. *J. Soc. chem. Ind., Lond.* **63**: 48-51, 4 figs.
- POTTER, C., 1935, An account of the constitution and use of an atomised white oil—Pyrethrum fluid—to control *Plodia interpunctella* Hb. and *Ephestia elutella* Hb. in warehouses. *Ann. appl. Biol.* **22**: 769-805.
- REED, W. D., and LIVINGSTONE, E. M., 1937, Biology of the tobacco moth and its control in closed storage. *Circ. U.S. Dep. Agric.* No. **422**, 38 pp., 11 figs., 6 tables.
- SALT, G., 1936, Experimental studies in insect parasitism. IV. The effect of superparasitism on populations of *Trichogramma evanescens*. *J. exp. Biol.* **13**: 363-75, 1 fig., 5 tables.
- WALOFF, N., and RICHARDS, O. W., 1946, Observations on the behaviour of *Ephestia elutella* Hb. (Lep. PHYCITIDAE) breeding on bulk grain. *Trans. R. ent. Soc. Lond.* **97**: 299-335, 5 figs.
- ZACHER, F., 1941, Beobachtungen über "Kornmotten." *Z. angew. Ent.* **28**: 466-76.

APPENDIX 1.

Length of life of moths.

1. In 1943, samples of moths were caught week by week (1.vi.-2.ix.) and isolated in the warehouse in 3×1 inch-tubes with grain. As a large number (370 ♂, 526 ♀) of moths was isolated, it can be taken that on the average the moths had already lived half their life when caught, so that the average length of life in the tubes was doubled to get the true length. This assumption is only valid when samples are taken throughout the emergence period, so that moths of all ages are taken in their true proportions and the seasonal cycle in temperature is also covered. The average lengths of life obtained in this way were, ♂ 19.9 days, ♀ 23.4 days. With a sex-ratio of 2 ♂, 3 ♀ (p. 258) the whole population would have an average length of life of 22.0 days.

2. In 1944, less extensive data were obtained by other methods. (a) Moths derived from larvae collected in the warehouse in autumn 1943 and

hibernated at Slough in an unheated outhouse were paired and kept in 3×1 -in. tubes. These moths gave the following data (Table 26).

The moths, both Slough-bred and in the warehouse, were much smaller in 1944 than in 1943, probably because their larvae had developed under

TABLE 26.

Sex	Nos.	Weight on emergence, mg.	Length of life, days
♀	34	7.8	12.5
♂	29	6.7	10.4

crowded conditions (see p. 283). A few warehouse moths probably already of some age weighed more than 10 mg. in 1943.

(b) Moths were brought back from the warehouse in 1944, weighed and kept at Slough in the unheated outhouse. The females could be divided into those which dissection after death showed had only paired once (see p. 261) and those

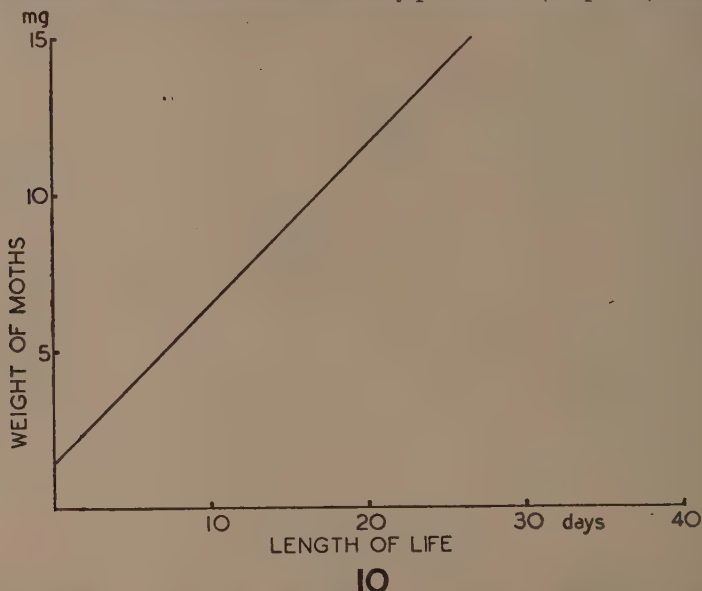


FIG. 10.—Relation between weight on emergence and length of life. Curve fitted by method of least squares, based on 34 Slough-bred warehouse larvae, kept in an unheated outhouse.

which had already paired twice or more. Ignoring the second group, there were 26 once-paired females. On the average, they weighed 8.5 mg. and lived 12.4 days. These must have lived at least one day in the warehouse before they were caught, so their true length of life was probably about 13.5 days. This figure is reasonable when these moths are compared with those in Table 26 where moths weighing 7.8 mg. lived 12.5 days. There is a direct relation between weight on emergence and length of life; see fig. 10.

With the males, the data are less good, since the younger ones cannot be picked out as in the females. The 23 warehouse moths studied on the average weighed 6.8 mg. and lived 8.6 days. Compared with Table 26, where moths weighing 6.7 mg. on emergence lived 10.4 days, the warehouse moths must have been considerably heavier when they emerged and must have lived more than 10.4 days. If it is assumed that the length of life of the sexes had the same proportion as in 1944, viz. 19.9 : 23.4, the length of the male can be put at $19.9 \cdot 13.5 = 11.5$.

The figures ♂ 11.5, ♀ 13.5, ♂♀ 12.5 days have been used in treating the 1944 data.

APPENDIX 2.

The accumulated total of moths in 1943, and average weekly number in 1944.

(a) The peak number of moths from the weekly counts was 37,300 on 1.vii.43. By this date, examining the weekly counts, given in Table 3 and taking the length of life as 22 days, 3000 would already have died, so the accumulated total to 1.vii. is 40,300. On 6.vii. the count was only 26,400, though only 1200 ought to have died, so there was a loss of $37,300 - 26,400 + 1200 = 9700$. It is thought too that these moths flew out of the windows between 1.vii. and 6.vii. Taking the net figure given on p. 261 of 32 (= 43 - 11) flying out per half-hour, allowing 3 hr. as the period of active flight, the number expected to fly out of 9 windows in 5 days would be 8600.

TABLE 27.

Methods of calculating numbers of "new" and "old" moths.

Date	Moth count (based on sample areas) on last date	Moths died between two dates	Moths surviving from pre- vious date	Moths emerged between two dates
24.v.-31.v.	600	—	0	600
31.v.-6.vi.	900	$990 (13 - 12.5) = 43$	$600 - 43$ $= 557$	$900 - 557$ $= 343$
6.vi.-14.vi.	900	$557 + 343 (14 - 12.5)$ $= 557 + 86 = 643$	$343 - 86$ $= 257$	$900 - 257$ $= 643$
14.vi.-21.vi.	1,300	$257 + 643 (15 - 12.5)$ $= 257 + 201 = 458$	$643 - 201$ $= 442$	$1,300 - 442$ $= 858$

The data obtained from moth counts in another room (2) in the same building were used to interpret the data from the main room (1). In room 2, the curve of emergence was exactly parallel to that of room 1, week by week, though the numbers were lower. The peak and the accumulated total in room 2 on 1.vii. was 27,400. Room 2 was sprayed with pyrethrum on 5.vii. and all but 600 of the moths were killed, but by 29.vii. another 16,500 had emerged. Therefore the ratio between the accumulated totals up to and after 1.vii. in room 2 was as 27.4 to 16.5. Applying this ratio to room 1, the estimated accumulated total is $(1 + \frac{16.5}{27.4}) 37,300 = 1.60 \times 37,300 = 59,700$ moths. Of these 35,800 were ♀, 23,900 ♂.

The method of calculating numbers emerging and dying in 1944 is briefly explained on p. 258. The following example shows how the method was applied in detail, using 12.5 days as length of life (Table 27).

TABLE 28.
Average daily numbers, ages, and oviposition of ♀, 6.vii.-19.vii.1944.

Age, days	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	Moth total = no. ♀ × 2	Total of eggs
% of eggs laid on this day															
6-7.vii.	12-2	20-5	14-2	13-1	9-3	7-9	5-5	4-1	3-9	2-4	2-7	1-8	2-4	—	—
7-8.vii.	7,254-96	8,495-39	8,495-39	8,495-39	8,495-39	8,495-39	8,495-89	8,495-39	8,495-39	596-78	596-78	596-78	295-39	—	—
8-9.vii.	"	7,254-96	7,254-96	"	"	"	"	"	"	8,495-39	"	"	"	—	—
9-10.vii.	"	"	"	7,254-96	7,254-96	"	"	"	"	"	8,495-39	"	"	—	—
10-11.vii.	"	"	"	"	7,254-96	"	"	"	"	"	"	8,495-39	"	—	—
11-12.vii.	"	"	"	"	"	7,254-96	"	"	"	"	"	"	4,247-70	197,499-60	—
Moth totals	43,529-76	44,770-19	46,010-62	47,251-05	48,491-48	49,731-91	50,972-34	50,972-34	43,073-73	35,175-12	27,276-51	19,377-00	5,739-65	—	—
Totals of eggs laid	483,267	885,188	594,549	563,280	410,383	357,523	255,117	190,178	152,869	76,822	67,018	31,741	12,535	—	4,030,470
Age, days	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	Moth total = no. ♀ × 2	Total of eggs
12-13.vii.	4,035-39	7,254-96	7,254-96	7,254-96	7,254-96	7,254-96	7,254-96	8,495-39	8,495-39	8,495-39	8,495-39	8,495-39	4,247-70	—	—
13-14.vii.	"	4,035-39	7,254-96	"	"	"	"	7,254-96	7,254-96	"	"	"	"	—	—
14-15.vii.	"	"	4,035-39	"	"	"	"	"	"	7,254-96	"	"	"	—	—
15-16.vii.	"	"	"	4,035-39	"	"	"	"	"	"	7,254-96	"	"	—	—
16-17.vii.	"	"	"	"	4,035-39	"	"	"	"	"	"	7,254-96	"	—	—
17-18.vii.	"	"	"	"	"	4,035-39	"	"	"	"	"	"	3,627-48	—	—
18-19.vii.	"	"	"	"	"	"	4,035-39	"	"	"	"	"	"	136,300-02	—
Moth totals	28,247-73	31,467-30	34,686-87	37,906-44	41,126-01	44,345-58	47,565-15	52,025-15	53,265-58	54,506-01	55,746-44	56,986-87	29,113-68	—	—
Totals of eggs laid	313,606	587,022	448,224	451,883	348,049	318,800	238,064	194,106	189,040	119,041	136,969	93,344	63,584	—	3,501,732

The calculations in column 3, may be explained as follows, *e.g.* for 14.vi.-21.vi. The figure 257 represents moths which emerged before 31.v. On 14.vi. all of these will be dead. To this figure must be added those which emerged between 6.vi. and half-way through 8.vi. (*i.e.* 21.vi.—12.5 days). Assuming (what is not strictly true) that emergence occurs at a uniform daily rate, the numbers emerging daily were $\frac{94.3}{8}$. This daily rate must be multiplied by $15 - 12.5 = 2.5$. Thus the total number of moths dying in the period is $257 + \frac{94.3}{8} \times 2.5 = 458$. The numbers of older moths (column 4) equals moths emerged in previous period less those that would have died, *e.g.* for the same two dates, $643 - \frac{94.3}{8} \cdot 2.5 = 442$. The number of moths emerged in a period is the difference between the moth count and the number of older surviving moths, *e.g.* $1300 - 442 = 858$.

(b) *Average daily number of ♀ moths in 1944.* The primary assumption necessary to calculate these figures is that moths both emerge and die at uniform rate over short periods. The figures for "old" and "new" moths in Table 3 have been used, but they were recalculated to two places of decimals, in order to obtain consistent results in Table 28.

The figure 7254.96 (row 1, column 1) = new ♀ moths on 12.vii. divided b interval 6.vii.-12.vii. (6)

$$= \frac{87,059.52}{2 \times 6} = 7254.96$$

8495.59 = new ♀ moths on 6.vii. divided by interval 29.vi.-6.vii. (7)

$$= \frac{118,935.47}{2 \times 7}$$

The figure 596.77 is obtained as follows. The 9548.41 "new moths" on 29.vi. include 4774.22 ♀ which emerged between 21.vi. and 29.vi., one-eighth of the number = 596.78 emerging each day. Those which emerged on 21.vi. to 23.vi. inclusive will be already dead. Of those which emerged on 24.vi. half (13-12.5) will be dead and half = 298.39 will survive. All those which emerged on 25.vi.-28.vi. inclusive will be alive. The other figures in the table are obtained by similar arguments.

Running across the top of the table are figures for the percentage of total fecundity realised on each day of life, taken from Appendix 3. All the moths in column one are in the first day of their life and will lay 12.2% of their total egg-number in that day. Thus for the period 6.vii.-12.vii. the 43,529.76 moths in column one will lay $\frac{12.2}{100} \times 91$ eggs each, and so on for the other ages.

APPENDIX 3.

Fecundity of moths in 1944, and related topics. Expectation of life in 1944 moths.

(I) Insufficient moths were studied to estimate fecundity directly as in 1943. The following data are available: (a) a number of warehouse larvae, collected in autumn 1943, were kept in an unheated outhouse at Slough. After pairing the resulting moths in tubes in the outhouse, 34 females had an average fecundity of 79. These females weighed on the average 7.8 mg., and were smaller than the warehouse moths of 1944. Figure 11 shows the relation between weight on emergence and subsequent fecundity in these Slough-bred moths. The line has been fitted to the data by the method of least squares.

(b) Many warehouse moths were brought back to Slough at about the time of the maximum moth-flight in 1944. Twenty-seven of these were found by dissection after death to have paired only once (half of them were actually *in cop.* when caught) and therefore were unlikely to have laid many eggs before capture. These moths weighed on the average 8.5 mg. and their average fecundity was 91. From fig. 11 it will be seen that for that weight a fecundity

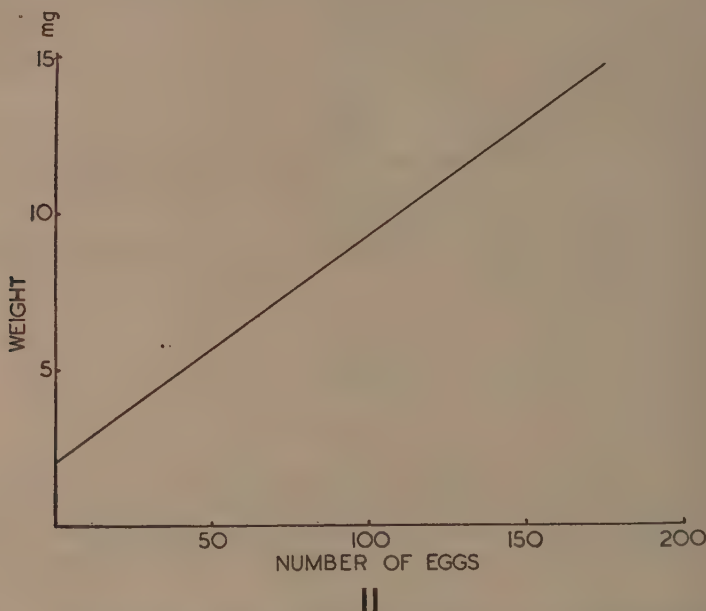


FIG. 11.—Curve showing relation between weight on emergence and fecundity in 34 Slough-bred moths.

of 87 would have been expected. The two sets of data are therefore reasonably consistent and the figure of 91 though rather unsatisfactory has been used in the calculations.

(II) *Percentage of total fecundity expected in moths of various ages.* These data are based on a study of 32 female moths bred in an unheated outhouse at Slough from warehouse larvae collected in autumn 1943. They laid 2491 eggs. The percentage of the total egg-number laid on each day of life is shown in Table 29.

From Table 29 can be calculated what percentage of its total number of eggs a moth of any age will lay in any subsequent number of days. Thus a moth three days old will lay on the average in the next four days, $13.1 + 9.3 + 7.9 + 5.5 = 35.8\%$ of its eggs.

(III) *Infertility of eggs.* In 1943, 21 ♀ moths from warehouse larvae collected in the spring were paired out-of-doors at Slough. They laid an average of 92 eggs, of which 86.5% hatched. In 1944, 33 moths from warehouse larvae collected in the spring were similarly paired. They laid an average of 79 eggs, of which 87.3% hatched. As these moths had no opportunity for a second

pairing, the infertility to be expected in the warehouse was somewhat less, and the figure of 10% has been adopted.

(IV) *Larval mortality in grain from trays* (Table 4) incubated at 25° C. The eggs from the trays of grain exposed in the warehouse were not counted until the grain had been incubated for 3-4 weeks at 25° C., by which time the larvae were big enough to count. During development some of the larvae die, the number largely depending on the degree of crowding. In experiments with single 1st stage larvae put on 35.0 g. of grain, none died in first 3 weeks. With 25 larvae on 200 g. 22.4% died in 4 weeks. With 150 or 200 larvae on 200 g. about 50% died in the same period (see p. 283).

TABLE 29.

Day of life of moth	Per cent. of total eggs laid on that day	Day of life of moth	Per cent. of total eggs laid on that day
1	12.2	8	4.1
2	20.5	9	3.9
3	14.2	10	2.4
4	13.1	11	2.7
5	9.3	12	1.8
6	7.9	13	2.4
7	5.5		
		Total	100.0

In calculating the number of eggs which gave rise to the larvae ultimately found in the "tray-grain," it has been assumed that 10% of the eggs were infertile and that 25% of the larvae died before the grain was examined. Thus, the number of larvae must be multiplied by 1.48 to get the number of eggs. In a few sets of trays on which oviposition was unusually heavy, the figure 1.48 is clearly too low (see p. 265).

APPENDIX 4.

Observations in 1945.

Some visits were made to the granary between 18.v. and 19.vii.45 by N. Waloff and J. Bowyer. The moths were counted on the usual areas with the following results.

Date	Estimated moth no.
18.v.	200
25.v.	200
31.v.	200
12.vi.	1,100
21.vi.	6,800
28.vi.	69,600
5.vii.	173,600
12.vii.	149,300
19.vii.	68,900

As in 1944, there was a small preliminary emergence in May which seemed to be independent of the main emergence. The peak of numbers fell on 5.vii., a date lying between the corresponding dates in 1943 and 1944. Assuming that the total emergence would be 1.6 times the peak number (p. 261), the estimate for this was $173,600 \times 1.6 = 277,800$.

The enormous discrepancy between this figure and the number of moths expected (about 1.5 million, Table 25) can only be due to a high mortality of larvae continuing into the spring, whereas in previous years mortality was very small after the winter. Collections of larvae from crevices made on 2.iii.45 and 12.vi.45 did in fact suggest that this was so.

The mortality figure was 38.5% for larvae alive on 2.iii. and 15.0% of the pupae died. Of larvae and pupae extracted from crevices on 12.vi., 83.6% were dead, suggesting a higher mortality than the 65% estimated up to 5.iv. (Table 10).

It seems probable that the effects of overcrowding in 1944 were more important than was supposed, and that 300,000 moths is about the maximum number the room is capable of supporting.

The moths continued to decline in weight as shown below.

Year	No.	Estimated weights		
		♀, mg.	No.	♂, mg.
1943	30	9.4	10	8.5
1944	26	8.5	—	[7.6] ¹
1945	99	6.9	56	6.1

¹ Estimated from 29 Slough-bred moths.

The average length of life of 48 ♀ taken *in cop.* on 28.vi. was 13.9 days. A similar figure for 17 males was 11.4 days but these were of unknown age. The average temperature during their survival period was 13.3° C. which is lower than that for the same period in 1944.

The sex-ratio in the warehouse from samples taken on various dates between 25.v. and 19.vii. was 184 ♂ : 217 ♀ = 1 : 1.2. There is no evidence of further progressive alteration of the ratio (p. 285).

Vol. 97. Part 12. Pp. 299-335, 5 figs.

30th October, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

	PAGE
WALOFF, N., Ph.D., and RICHARDS, O. W., M.A., D.Sc. Observations on the behaviour of <i>Ephestia elutella</i> Hübner (Lep., PHYCITIDAE) breeding on bulk grain	299-335, 5 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 12s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBS, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

OBSERVATIONS ON THE BEHAVIOUR OF *EPHESTIA ELUTELLA*
HÜBNER (LEP., PHYCITIDAE) BREEDING ON BULK GRAIN

By Miss N. WALOFF, Ph.D., and O. W. RICHARDS, M.A., D.Sc.

Manuscript received 24th September, 1945.

(Read 5th June, 1946.)

WITH 5 TEXT-FIGURES.

CONTENTS.

	PAGE
I. Observations on the behaviour of moths	300
A. Oviposition	300
B. Reactions of moths to light and periodicity of activity of the moths	303
C. Distribution of moths in temperature gradients	312
D. Reactions of moths to air currents	315
II. Observations on the behaviour of larvae	316
A. Distribution of feeding larvae	317
B. Observations on wandering larvae	329
III. Discussion	333
IV. Acknowledgements	333
V. General Summary	334
VI. References	334

DURING 1941-44 an infestation of bulk wheat by the moth *Ephestia elutella* Hübner was studied in a London granary. The principal purpose of the work (Richards and Waloff, 1946) was to study the changes in the moth population throughout the season and from year to year. In the course of the main work a number of behaviour problems were encountered and some of these had to be studied in order to devise reliable methods of sampling the population. The present paper records the observations and experiments on behaviour which are not so extensive as they would have been if the main work had lain in this field. All warehouse observations were made jointly but all laboratory experiments are the work of N. Waloff.

The granary consists of a large number of rooms 100 × 50 × 8 ft. in which grain is usually stored to a depth of 4-6 ft. The rooms have a number of windows, but when full there is insufficient light for reading except quite near windows, and much of the room is dark. The ceiling is supported by four rows of eight pillars connected longitudinally by pairs of large beams. Between the rows of beams are four rows of large pipes through which grain can be poured into or out of the room. The bulk of grain largely controls the temperature and humidity of the rooms. A fuller account of one particular room will be found in Richards and Waloff (1946).

Temperature was recorded either in two or three places with recording thermographs or, when many measurements were required, the air temperature was read from the dry bulb of a whirling psychrometer. Relative humidity was recorded at one place on a hygrograph and occasionally by a number of measurements with a whirling psychrometer. Water content estimations of the

grain were also sometimes made; these can be converted into relative humidities. Light was measured with a Holophane lumeter kindly lent by Dr. W. D. Wright of the Physics Department of the Imperial College of Science and Technology. Air currents were measured with an air meter in which the movements of the vanes could be timed to give readings in feet per second. Except near open windows, air movement was too small to be measured. All times mentioned are Greenwich mean time.

I. OBSERVATIONS ON THE BEHAVIOUR OF THE MOTHS.

(A) *Oviposition.*

The pre-oviposition period following pairing lasts in most females over 24 hours. Most of the eggs are laid in the first 4 days of life. These aspects of the biology of the moths are discussed in another paper (in preparation).

(i) *Time of oviposition.* The following observations on the time of oviposition were made on 14 fertilised females kept under a glass bell-jar standing on crumpled black tissue paper, which provided the oviposition site. The paper was renewed every six hours (at 3 a.m., 9 a.m., 3 p.m., and 9 p.m.), and the eggs were counted. Previous observations had shown that the moths

TABLE 1.
Number of eggs laid by 14 ♀ moths at 6-hourly periods.

Date	9 a.m.-3 p.m.	3 p.m.-9 p.m.	9 p.m.-3 a.m.	3 a.m.-9 a.m.
1.viii.44 . . .	—	34	47	0
2. " . . .	0	65	63	1
3. " . . .	0	36	57	10
4. " . . .	15	118	105	0
5. " . . .	0	33	81	6
6. " . . .	3	36	12	0
7. " . . .	0	12	14	0
8. " . . .	0	—	—	—
Total . . .	18	334	379	17
% of total . .	2.3	44.6	50.7	2.3

prefer rough to smooth surfaces for oviposition, and the 63 eggs laid on glass out of the total of 811 were not included in the egg count. The bell-jar was kept in a dark part of the room where the maximum light intensity did not exceed 2 F.C., and approximated to that of a warehouse room. The results clearly show that the range of light intensities which immobilises the moths during the day also determines the period of oviposition—most of the eggs being laid at night. Table 1 shows the numbers of eggs laid by the moths in different 6-hourly periods of each 24 hours.

(ii) *Warehouse observations.* The moths are weakly negatively phototactic and tend to aggregate in the darker parts of the room. There are two distinct periods of flight every 24 hours at the changing light intensities of sunset and sunrise, when the males take to wing before pairing. The females are relatively inactive and fly much less than the males. Although laboratory observations suggest that most of the eggs are laid in the evening and at night, the inactive females tend to oviposit near the sites in which they aggregate in daytime, *i.e.* in the darker areas of the room. The full data on oviposition in the warehouse are given in the population study, but it may be mentioned here

that in 1943, 30 shallow 1-sq. foot trays, covered with a layer of grain, were exposed to different light intensities ranging between 1.1 F.C. and below 0.0001 F.C. The grain on the trays was changed every week for a period of 8 weeks and incubated at 25° C. 70% R.H. The larvae from the eggs were counted when they were big enough for this to be easy. An allowance for 25% mortality (usual in laboratory experiments) was made. In 1944, 19 such trays were exposed for two successive weeks. A very clear negative correlation between light intensity and the amount of oviposition measured on exposed grain samples in different parts of the room was obtained in 1943 ($r = -0.6931$, $p < 0.01$, $n = 28$). No such clear correlation was seen in 1944, although again the greatest numbers of eggs were laid on sample areas near which the maximum numbers of moths had been noted in the weekly counts (see Richards and Waloff, 1946). However, in 1944 relatively more eggs were laid near the windows. In 1943 the windows of the room were open, whereas in 1944 they were closed, and this may explain the difference noted between the two years. This made little difference to the dim lighting of the room, but the air currents were cut off, and it may be that these were avoided by ovipositing females in 1943.

(iii) *Laboratory observations on the choice of oviposition sites.* The preferred oviposition sites were determined, using a number of likely alternatives. The moths were introduced into a circular glass dish 6 cm. high and 20 cm. in diameter; the alternative oviposition sites formed the floor of the apparatus. The glass dish was kept in complete darkness. The results obtained from experiments on isolated moths closely correspond to those obtained from groups of moths, and it is thought that crowding had no effect on the choice of sites. The groups of moths were left for four days in the apparatus and the eggs on the different surfaces were then counted. The results of these experiments are summarised in Table 2.

In the absence of sacking and grain most of the eggs were laid in narrow crevices, and only a few on flat surfaces of glass, wood and brick. Sacking over grain was preferred to sacking over glass beads, and over KOH at 70% R.H., i.e. of the same humidity as the wheat. When open grain was presented as an alternative to sacking or sacking over grain, over 80% of the eggs were laid on it. This indicates a strong reaction, mainly chemotactic, by the ovipositing females. Crombie (1941) found that in *Rhizopertha dominica* Fabricius, the sense of smell was the most important factor in leading the insect to an environment where food was present. He also says that once the insect was in an environment having the odour of food, the sense of touch appeared paramount in selection of oviposition site. This also appeared true of *Ephestia* moths presented with open grain as an alternative to sacking over grain; for while the smell of grain permeated the whole of the small glass vessel, most of the eggs were laid on open grain. However, it has also been found that the females will oviposit readily in empty glass tubes. Similar results were obtained when the oviposition sites were presented to isolated females; these are summarised in Table 3.

All the moths in these experiments were reared as larvae on middlings and this larval food might have had an effect on the choice of the site by habituation in the sense of Thorpe (1943). Control experiments were made in which half of the moths were reared on cacao and half on grain. Isolated fertilised females were put into glass jars containing small shallow tins with cacao beans or grain, covered with muslin tightly stretched over the tops. Of the 13 females reared on cacao—6 laid on the muslin of the cacao tins only, 4 laid most of

TABLE 2.

Choice of oviposition sites by moths of *Ephestia elutella*.

No. of exp.	Temperature, ° C.	No. of ♀♀	Total egg number	No. of eggs on oviposition sites							
1	18-21	40	1598	Glass dish in contact with Wood			Crevice		Flat surfaces		
				Brick	Wood-side	Brick-side	Glass	Wood	Brick		
				197	261	375	289	55	191	230	
				70.2%			29.8%				
2	15-19.5	25	1263	Glass dish in contact with Brick		Crevice between 2 bricks		Flat surfaces			
				Sacking			Glass	Brick	Sacking		
				8	12	204	12	155	872		
				17.7%			0.9% 12.2% 69.2%				
3	15-19.5	25	707	Glass dish in contact with Wood		Crevice between 2 blocks of wood		Flat surfaces			
				Sacking			Glass	Wood	Sacking		
				11	8	101	24	87	476		
				16.9%			3.4% 12.3% 67.3%				
4	18-21	15	980	Sacking over wheat at 70% R.H.				Sacking over air			
				572				408			
				58.4%				41.6%			
5	16-23	25*	1056	Sacking over wheat at 70% R.H.				Sacking over KOH at 70% R.H.			
				624				432			
				59.1%				40.9%			
6	18-21	25	1476	Sacking over wheat				Sacking over glass beads			
				976				500			
				66.8%				33.2%			
7	16-23	25	1208	Open wheat grain				Sacking over air			
				1028				182			
				84.9%				15.1%			
8	17-20	50	3157	Glass	Open wheat grain		Sacking over wheat				
				119	2749		289				
				4.1%	87.1%		8.8%				

TABLE 3.

Choice of oviposition sites by isolated ♀ moths (6 in each experiment).

Exp. 1			Exp. 2			Exp. 3		Exp. 4		Exp. 5		Exp. 6		Exp. 7	
Number of eggs on															
Glass	Wood	Brick	Sack- ing	Wood	Sack- ing over grain	Sack- ing over air	Sack- ing over grain	Sack- ing over grain beads	Sack- ing over 70% R.H. grain	Sack- ing over 70% R.H. KOH	Open grain	Sack- ing	Open grain	Sack- ing over grain	
0	8	9	4	0	12	0	89	8	25	0	78	0	13	4	
0	16	6	9	0	5	3	81	32	26	0	42	0	13	0	
17	49	4	2	0	43	19	34	0	97	0	8	14	94	0	
0	23	1	57	0	58	3	12	2	2	4	50	0	94	0	
0	35	6	10	0	41	30	14	5	2	5	32	44	17	0	
0	20	17	32	1	31	27	29	14	2	10	75	25	7	0	
17 8.4%	151 71.3%	43 20.3%	114 99.1%	1 0.9%	190 69.8%	82 30.2%	259 80.9%	61 19.1%	154 89%	19 11%	285 77.4%	83 22.6%	238 98.3%	4 1.7%	

the eggs on cacao tins and some on grain tins, and 3 others laid more on the muslin of the grain tins. In the experiments with the 14 females reared on grain, 4 of them laid on the cacao tins only, while the remaining 10 laid on both tins, but in each case the majority of eggs was laid over cacao. Thus, the strongly smelling cacao attracted most of the ovipositing females, irrespective of whether the larvae were reared on cacao or on grain. These results are given in Table 4.

Bovingdon (1933) reports a higher number of moths caught in traps with tobacco extracts than in those containing extracts of cacao.

(iv) *Warehouse observations.* A striking example of chemotaxis of the moths towards grain was observed at the time of the maximum moth numbers in the warehouse. Ten 7-lb. jars, each containing 200 g. of grain, were put under elder bushes at a distance of 50, 100 and 150 yards away from the granary. The jars were protected against rain by wooden roofs raised on wires. The grain was changed every fortnight (21.vi.-31.viii.44) and incubated at 25° C. Nine out of the 40 sets of grain so examined had larvae or eggs of *E. elutella*, and dead *E. elutella* moths were found in 5 of them.

TABLE 4.

Temperature	No. of females	Larval food	No. of eggs laid on muslin of	
			cacao tins	grain tins
25° C. 70% R.H.	13	Cacao beans	435 79.8%	110 20.2%
25° C. 70% R.H.	14	Wheat grain	530 77.4%	155 22.6%

Summary of observations on oviposition.

1. The pre-oviposition period following pairing lasts about 24 hours.
2. Most of the eggs are laid in the first 4 days of female life.
3. Laboratory observations suggest that oviposition takes place in the evening and at night.
4. As the moths are weakly negatively phototactic, and the activity of the females is restricted, there is a tendency for most of the eggs to be laid in the areas of the storage room which are the darkest by day.
5. There are indications that air currents near windows are avoided by ovipositing females (see also p. 315).
6. Laboratory experiments on the choice of oviposition sites show that the order of preference is open grain, sacking over grain, sacking, crevices and lastly flat surfaces such as wood and glass.

A striking example of chemotaxis towards grain was also obtained in warehouse observations.

7. The ovipositing females are more strongly attracted towards the smell of cacao beans than grain, irrespective of whether the larvae of the moths were reared on cacao or grain, i.e. there appears to be no habituation.

(B) *Reactions of moths to light and periodicity of activity of the moths.*

- (a) *Warehouse observations.* The largest numbers of moths are seen in the darker parts of the storage room, although some can always be found at all

light intensities. There are numerous references in literature to the preference of adults for dark corners (Mossop 1932; Munro and Thomson 1929; Regnier 1932; Skalov *et al.* 1936). The behaviour of the weakly negatively phototactic moths is complicated in several ways: (i) the negative phototaxis is strongly marked only below a light intensity of 0.1 F.C.; (ii) moths are immobilised by diffuse daylight; (iii) there is a reversal or loss of negative phototaxis with age—larger numbers of older moths are found in the lighter areas of the room.

The distribution of moths in different light intensities is summarised in Table 5. When the correlation coefficient between the distribution of moths in a dimly lit room (light intensity 0.144–0.0003 F.C.) was worked out it was significant, i.e. r was -0.4145 , $n = 37$, $p = <0.01$. In a lighter room (35.0–0.03 F.C.) the correlation between the distribution of moths and light intensities

TABLE 5.

Description of area	Sample area as % of total area	Date	Total no. of moths recorded	Range of light, F.C.	Numbers of moths per area expressed as % of total				
					1 F.C. over	0.9–0.1	0.09–0.01	0.009–0.001	0.0009–0.0001
1. Walls: room with wheat	4	Weekly samples 21.vi.–26.viii.43	3,496	0.8–0.003	—	14	26	60	—
2. Walls: room with wheat	4 ¹	Weekly samples 5.v.–24.viii.44	9,974	0.122–0.0019	—	13	42	45	—
3. Ceiling: room with wheat	1.5	Weekly samples 21.vi.–26.viii.43	2,831	1.0–0.001	20.5	—	21.5	58	—
4. Ceiling: room with oats	6	8.vi.43	414	0.144–0.0003	—	4	20	12	64
5. Ceiling: same room as (4)—but empty	6	24.vi.43	585	1.4–0.0045	0	1.1	3.4	94.5	—
6. Ceiling: empty room	20	14.vii.44	665	35.0–0.03	10	30	60	—	—
7. Ceiling: room with wheat	4.5	Weekly samples 5.v.–24.viii.44	16,499	0.028–0.001	—	—	66.8	33.2	—

Correlation coef. moth numbers with light 4: dim room light int. 0.144–0.0003 F.C., $r = -0.4145$, $n = 37$, $p < 0.01$.

Correlation coef. moth numbers with light 6: lighter room 35.0–0.03 F.C., $r = -0.2993$, $n = 113$, $p < 0.01$.

was again significant: r was -0.2993 , $n = 113$, $p = <0.01$, i.e. in spite of the difference in the ranges of light intensities, the greater numbers of moths were found in the darker areas of the two rooms. Similar results can be seen in Table 5. In one set of observations (ceiling 1944, Table 5), the light intensity was more uniform than usual, and no significant correlation was found. This may have been partly due to unusually high moth-density inducing a more uniform distribution.

However, the aggregations of moths in dark areas are not entirely due to the negative light reaction of the adults, but also to a strongly marked negative phototaxis of their larvae, which tend to move into the darker areas before spinning up in crevices. Moreover, the flight of the females is somewhat restricted and they tend to oviposit near the places of emergence, i.e. in the darker areas. Thus the negative phototaxis of the adults and larvae, together with the restricted flight of females, combine in the building up of populations in the areas of low light intensity.

The negatively phototactic reaction of the adults is either altered or lost as the moths grow older; thus the length of life of the female and male moths caught and isolated in tubes was on the average shorter in moths from light than from dark areas (see Richards and Waloff, 1946).

Date		Sex	No. of moths	Average length of life
10.vi.-5.viii.43	Dark areas	♀	228	24.3 days
"	"	♂	118	21.6 "
"	Light areas	♀+♂	177	21.6 "
"	"	♂	170	18.0 "

This suggests that the alteration in the reaction occurs in the course of 3-4 days of the life of moths, and the suggestion is borne out by laboratory observations. The average weight of 139 moths collected on 21.vi.45 from the lighter areas of the room was lower than of those from the darker, again indicating that these moths were older.

The average weight of 42 females from dark areas was 6.98 mg.

"	"	"	"	40 females	"	light	"	"	5.7	"
"	"	"	"	30 males	"	dark	"	"	5.66	"
"	"	"	"	27 males	"	light	"	"	4.87	"

These results are statistically significant, and when the significance of the variance of means was worked out for females, p was <0.01 , and for males p was <0.02 . These differences are not due to the larger moths aggregating in the dark areas, as when random samples of 17 females from light and 17 from dark areas and 18 males from light and 18 from dark areas were taken, the wing lengths of the moths from the light areas were actually greater than those from the dark, indicating that these were the larger moths, although not significantly so (for females p was <0.2 , for males p was <0.7).

The average wing lengths of these moths, measured from the proximal end of the retinaculum to the apex of the fore-wing on ventral surface, were as follows :—

17 females from dark areas	5.87 mm.
17 females " light	6.04 "
18 males " dark	5.73 "
18 males " light	5.96 "

(b) *Laboratory observations on reactions of moths to light.* Description of apparatus: two boxes, one measuring 36 in. $\times$ 9 in. $\times$ 8.5 in. and the other 72 in. $\times$ 10.5 in. $\times$ 10.5 in., painted black inside with one glass end and a glass front (36 in. or 72 in. long), were set up for the experiments. The front was directed towards the window. Each box was divided into 5 equal sections, each having a different intensity of light. The light gradient was produced by a screen consisting of 4 panels placed over the glass front. The gradient was produced in the following way :—

1. Direct light through glass front and end.
2. Light through one thickness of muslin.
3. Light through 8 thicknesses of muslin.
4. Light through black tissue paper.
5. Thick black paper admitting no light.

A thermometer was placed in each section, but no variations in temperature inside the boxes were noted at each reading [T° limits (1° C. or less at any one reading) 22—13.5° C. in Set I; 18.8—14° C. Set II; 18—9° C. Set III].

Freshly hatched moths were used. Laboratory stock in Set I and warehouse stocks in Sets II and III. Moths of both sexes were introduced into the boxes, and light readings and moth positions recorded 24 hr. later. Three

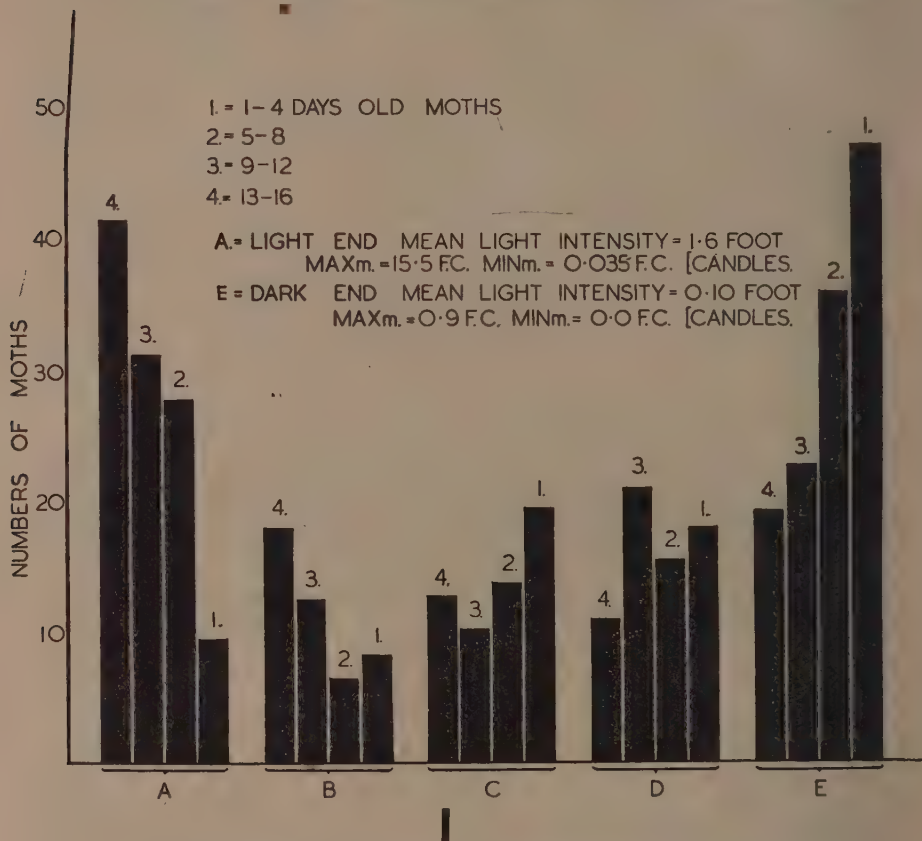


FIG. 1.—Numbers of moths in five sections of light choice-chamber, recorded separately for four ages of the moths.

readings were taken daily in Set I at 9 a.m., 1 p.m. and 4 p.m., and two daily readings at 9 a.m. and 1 p.m. in Sets II and III. Each reading consisted of (a) number and positions of moths in each section, (b) temperature, (c) light intensity in foot candles. Light intensities were read by focussing the lumeter through the glass end on to the back of each section. The screen was raised when the moths were counted. The experiments were continued until all the moths were dead and the position and sex of dead moths was recorded. The illumination was daylight for each particular day.

(c) *Results.* The life of the moths was divided into four-day periods. As numbers of live moths grew less from day to day they were expressed as a percentage of the total for each reading. Since the illumination varied from day to day and at different times on each day, what was measured was the proportion of the moths in the lightest and darkest parts rather than the aggregates at particular light intensities. The readings for each of the five compartments were added up over each of the three sets of experiments and the totals are shown graphically in fig. 1. The range of intensity and the mean intensities of the sections were as follows: Section 1. 15.5–0.035 F.C. (mean 1.6 F.C.); 2. 3.5–0.0045 F.C. (mean 0.589 F.C.); 3. 3.0–0.004 F.C. (mean 0.305 F.C.); 4. 2.0 F.C.—no reading possible (mean 0.173 F.C.); 5. 0.9—no reading possible (mean 0.1 F.C.).

The movement of the moths as they grow older, from the darker to the lighter parts, is clearly shown in the figure. Although the adding together of

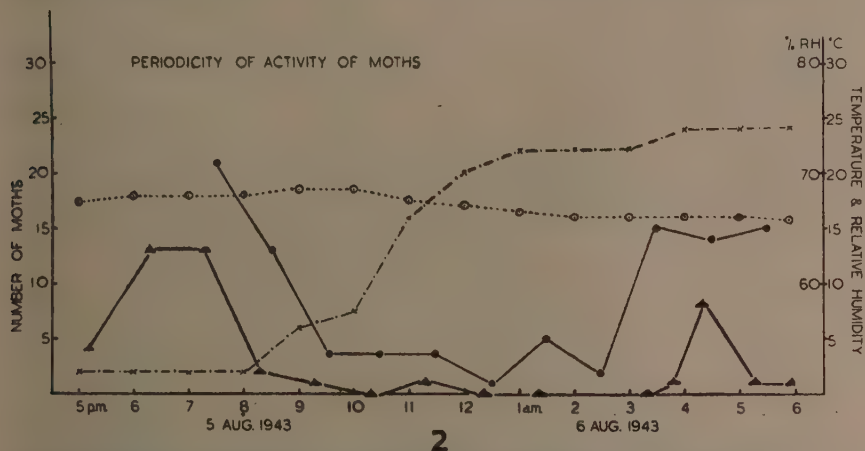


FIG. 2.—Warehouse observations 5–6.viii.43, numbers of moths leaving “chalk rings” ———. Numbers of moths flying in a ten-second beam of torchlight ▲—▲. Temperature ○.....○ Relative humidity ×.×.

readings at different light intensities might seem an uncertain measure of reaction to light, yet the aggregations detected in this way are probably similar to those observed in a warehouse lit by variable daylight. It is probable that some of the young moths may be immobilised by light greater than 1 F.C. at the light end; also the simple light-reaction is at first somewhat interfered with by pairing activities. At the end of the experiments, the position of dead moths was recorded. The numbers of these in each section were as follows:— 1. 9 ♂, 6 ♀; 2. 3 ♂; 3. 2 ♂, 1 ♀; 4. 3 ♀; 5. 5 ♂, 6 ♀.

(d) *The akinetic effect of diffuse daylight.* Diffuse daylight immobilises moths, and they tend to be quiescent at uniform light intensities above 1 F.C. In lower light intensities there is a certain degree of movement throughout the day. These movements are slight, and cannot be compared with the flight of moths at dawn and at dusk. On several occasions chalk rings were drawn around the moths sitting in different light intensities, and many more moths left these rings in the darker areas than in the lighter ones. The results of these observations are summarised below (Table 6).

TABLE 6.

Light intensity (judged by eye)	Light	Half-light	Dark
No. of "ringed" moths	26	26	26
No. moved out of rings between 9 a.m. and 2 p.m.	6	6	16
Same expressed as %	23	23	61

On another occasion chalk rings were drawn around 256 moths, and hourly observations were made between 10 a.m. and 6.30 p.m. Below is a summary of these observations.

TABLE 7.

	Light	Half-light	Dark
Range of light	0.25-7.7 F.C.	0.011-0.16 F.C.	0.0036-0.008 F.C.
No. of "ringed" moths	76	101	79
No. moved out of rings between 10 a.m. and 6.30 p.m.	33	55	58
Same expressed as %	43	54	73

The moths in the darker parts of the room were also much more easily disturbed than those in brighter light, and many more flew away whilst chalk rings were drawn around them than in the higher light intensities. For instance, on one occasion, while chalk rings were drawn,

1 out of 51 moths, *i.e.* 1.9%, flew away in light areas,
 6 " " 81 " " 7.4% " " " half-light areas,
 22 " " 75 " " 29.3% " " " dark areas.

This again illustrates the akinetic effect of diffuse daylight, which has been repeatedly observed in the laboratory.

(e) *Periodicity of activity of moths.* At sunset and at sunrise, that is, at changing light intensities, the moths begin to fly in areas of the room with intensities below 1 F.C. With the fall of light the flight becomes more generalised and large numbers swarm in darker areas. In the morning this flight starts out of doors. On one occasion many moths were seen on the wing outside the warehouse at 4 a.m. when light intensity was 0.7 F.C., but the number dropped markedly by 5.15 a.m. when light intensity had risen to 3.0 F.C. By that time the flight had spread to the dim warehouse rooms. Both in the evening and in the morning the males are much more active than the females, and although copulating moths are seen at any time of the day—the flight is a prelude to increased pairing. On two occasions when moths were caught and sexed the majority of males were on the wing, and the majority of females at rest.

Dates	Time	Flying moths		Resting moths	
		♂	♀	♂	♀
22.vii.43 and 5.viii.43	6-7 p.m.	38	17	32	54
		(69% : 31%)		(39% : 61%)	
5.viii.43	4.15-5.0 a.m.	13	12	5	20
		(52% : 48%)		(20% : 80%)	

As the sex ratio of moths in 1943 was as 2 ♂ : 3 ♀ (see Richards and Waloff, 1946), the proportion of flying males was even greater than is immediately apparent.

TABLE 8.

Area : 5 ceiling areas, 12 sq. ft. each. Moths ringed at 7 p.m.

Date : 5.viii.43.

Number of moths moved out of rings and new arrivals										
7-7.50 p.m.	7.50-8.50 p.m.	8.50-9.50 p.m.	9.50-10.50 p.m.	10.50-11.50 p.m.	11.50 p.m.-12.50 a.m.	12.50-1.50 a.m.	1.50-2.50 a.m.	2.50-3.50 a.m.	3.50-4.50 a.m.	5-6 a.m.
21	13	4	4	4	1	5	2	15	14	5

TABLE 9.

No. of moths in 10-second beam.

Date : 5.viii.43.

7 p.m.	8 p.m.	9 p.m.	10 p.m.	11 p.m.	12 p.m.	1 a.m.	2 a.m.	3 a.m.	4 a.m.	5 a.m.	6 a.m.				
4	0	0	0	0	0	0	0	0	4	2	1				
5.10 p.m.	6.10 p.m.	7.10 p.m.	8.10 p.m.	9.10 p.m.	10.10 p.m.	11.10 p.m.	12.10 a.m.	1.10 a.m.	2.10 a.m.	3.10 a.m.	3.50 a.m.	4.10 a.m.	5.15 a.m.	6 a.m.	
4	13	13	2	1	0	1	0	0	—	0	1	8	1	1	
7.30 p.m.	8 p.m.	9.10 p.m.			12.10 a.m.					4.10 a.m.	4.45 a.m.				
18	8	0	—	—	0	—	—	—	—	24	7				

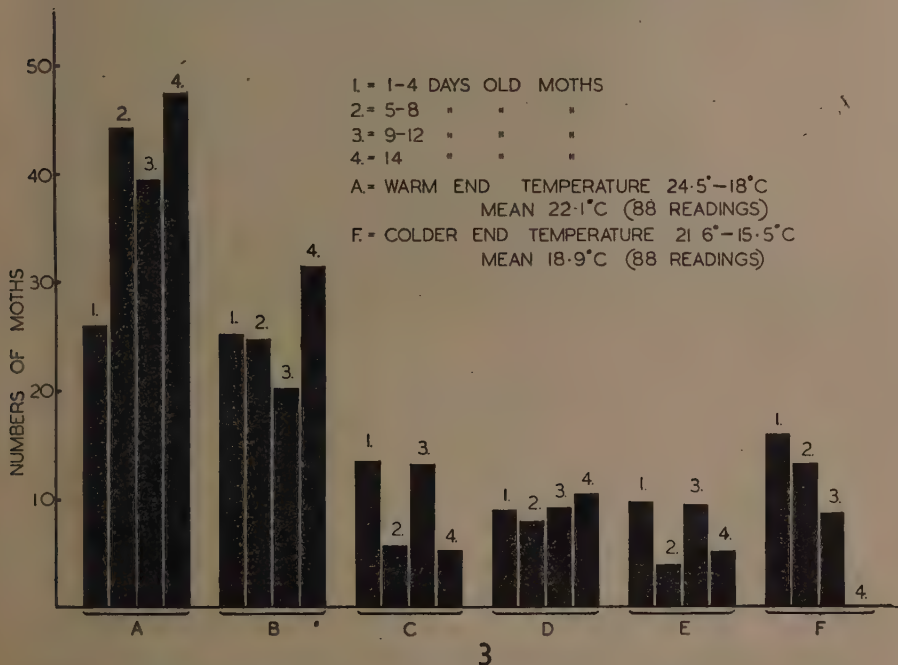


FIG. 3.—Numbers of moths in six sections of temperature choice-chamber, recorded separately for four ages of the moths.

This flight may not be independent of changes in temperature in outdoor conditions, but it has been seen in the laboratory when the temperature remained constant throughout the period of flight. The temperature, and to some extent relative humidity, are largely controlled by stored grain, and almost uniform conditions have been recorded for a week or more at a stretch. An attempt at estimating the periodicity of activity in the warehouse was made by chalking rings around the moths and noting the numbers which left the rings at intervals of time; also by counting the number of moths flying in a 10-second beam of torchlight in selected parts of the room. These results are summarised in the Tables 8 and 9 below, and fig. 2.

The moths become very active with the fall of light and especially when slanting rays of the setting sun penetrate into a room. The flight appears "aimless" and many moths hover up and down in one region. Where shadows are sharply marked off from the adjacent lighter areas, for instance under beams supporting the ceiling, flying moths are restricted to these darker parts and will turn back into the shade when they fly out into the light. Several sets of light readings were taken in these observations, and the following will serve as an example. On 22.vii.43 at 4.15 p.m. moths were swarming in a shadow cast by a wooden beam, where light intensity varied between 0.167 and 0.092 F.C., and only a few moths were seen on the wing in the adjacent area where incident light varied between 1.63 and 0.86 F.C. Later, on the same day, no moths at all were flying in light intensities between 6 and 1.2 F.C., but they were flying in shadows of 0.062-0.055 F.C. At the same time numerous moths were flying at a short distance from the ceiling and hovering above a floor the light intensity of which was 0.56 F.C.

Although there are two main flights every 24 hours, swarms of moths have been seen throughout the day on very hot days and in a room with heating grain, where the temperature of the air varied between 19 and 22° C. In 1944 there were very large numbers of moths in the storage room, and overcrowding and, presumably, mutual stimulation produced fairly large flying groups of moths even in daytime in the dim room, where light intensity rarely exceeded 1 F.C. even near the windows.

Although in daytime moths appear to avoid air-currents, during the flight period at dusk some may be seen to approach windows and fly out of them. Thus on a summer evening 54 moths were seen flying in and out of one window in 30 minutes. It is probable that the spreading of populations occurs at these periods of activity.

Laboratory observations on the activity of moths induced by falling light at constant temperature.

These observations, made in December, January and February, do not differ substantially from those made in the warehouse in summer, except that the activity was first noted at higher light intensities, and that the temperature of the laboratory remained almost constant and varied within 1° C. at most, at any one observation. In winter the period of rapid light change and hence of activity of moths was shorter. The moths remained immobile in diffuse daylight. Readings were taken every 30 seconds, as soon as activity was observed. The greatest possible amount of activity was measured by multiplying the number of moths by the number of readings; the actual activity (*i.e.* the number of moving moths multiplied by readings) was expressed as a percentage of the possible for the period.

TABLE 10.
Photokinetic effect of falling light on moths of *Ephestia elutella*.

Number of moths	Time and date	Greatest possible activity	Actual activity	% of possible activity	Tem-perature, ° C.	6-minute period												Light in F.C. No. of moving moths. % of inactivity.
						1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	
I. 9 ♂	3.15-4.27 p.m., 29.II.44	1296 moves	204 moves	15.7	17	15.0	—	10.0	8.0	—	5.0	2.5	1.5	0.6	0.2	0.07	0.025	Light in F.C. No. of moving moths. % of inactivity.
						4	2	0	7	4	16	13	27	28	36	32	—	
II. 10 5 ♂, 5 ♀	3.25-4.19 p.m., 19.XII.44	1000 moves	302 moves	20.2	13-14	96.3	98.1	100	94.5	96.3	85.2	88.0	75.0	75.0	66.7	70.4	67.6	Light in F.C. No. of moving moths. % of inactivity.
						7.0	6.75	4.0	2.0	1.4	0.6	0.45	0.325	0.09	—	—	—	
III. 12 6 ♂, 6 ♀	4-4.36 p.m., 1.I.45	864 moves	132 moves	15.3	19	0.13	0.08	0.02	0.006	0.003	0.005	—	—	—	—	—	—	Light in F.C. No. of moving moths. % of inactivity.
						0.08	0.02	0.006	0.003	0.001	*	—	—	—	—	—	—	
IV. 25 12 ♂, 13 ♀	4-5.4 p.m., 7.II.44	3200 moves	551 moves	17.2	19-19.5	84.7	83.3	70.1	79.9	90.3	100	—	—	—	—	—	—	Light in F.C. No. of moving moths. % of inactivity.
						15.0	2.6	0.6	0.5	0.25	0.56	0.2	0.12	0.05	0.005	4-min. period	*	
V. 10 5 ♂, 5 ♀	4-5.6 p.m., 22.I.45	1320 moves	200 moves	15.2	18	7	1.25	58	78	78	54	51	38	48	32	10	—	Light in F.C. No. of moving moths. % of inactivity.
						28	76	—	—	—	—	—	—	—	—	—	—	
						90.7	74.7	80.7	74	74	82	83	87.4	84	89.4	96.7	—	Light in F.C. No. of moving moths. % of inactivity.
						10.25	8.0	—	2.5	1.6	1.0	0.45	0.2	0.07	0.007	—	—	
						0	28	43	30	2	0.75	0	0.14	0.20	52	23	1	Light in F.C. No. of moving moths. % of inactivity.
						100	76.7	64.2	75	98.4	99.6	100	83.3	56.7	80.8	99.6	99.6	

* No reading possible.

Five sets of such observations, on one-day-old moths, are given in Table 10, where the activity increased with the fall in light intensity, and in Sets II and IV again decreased on approach of complete darkness. Only walking, hopping, or flying moths were recorded as active; "calling" females and moths with vibrating antennae were not included. The higher degree of activity in Set II was associated with mating, as 6 pairs were formed in this period of observations. The mating behaviour of the moths is similar to that of *Ephestia kühniella* Zeller described by Norris (1932). On the whole it would appear that this periodicity of activity is not caused by an inner rhythm but is a photokinetic reaction; for the time of activity seems to depend on light rather than the time of the day.

Barnes and Kaloostian (1940), who investigated the flight habits of dried-fruit insects in California, state that the nightly flight of *Ephestia figulilella* Gregson began half an hour after sunset and continued until sunrise, unless stopped by low temperature. The males outnumbered the females during the flight period. The same results are quoted for *Plodia interpunctella* Hübner and *Ephestiodes nigrella* (Ragonot). In *Ephestia kühniella* all the specimens caught were males.

The effects of light and temperature on rhythms in activity have recently been investigated by a number of authors (D. L. Gunn, 1940; K. Mellanby, 1940; I. D. Strel'nikov, 1940; and C. B. Williams, 1939). Stein-Beling (1935) considers that the rates of metabolism of the body determine the times of activity in social insects, and that this time-memory is independent of external periodicities.

Summary of the data on the distribution of moths at different light intensities and on periodicity of activity.

1. Moths of *E. elutella* are weakly negatively phototactic.
2. There is an alteration in the reaction to light in older moths.
3. Moths are inactive in diffuse daylight greater than 1.0 F.C.
4. Aggregations of moths in dark areas are partly due to the negative phototaxis of the larvae of the previous generations, and to the restricted flight of female adults.
5. There are 2 periods of activity in 24 hours—at changing light intensities at sunset and sunrise. This activity may be partly dependent on temperature, but laboratory data show that light alone is a sufficient stimulus.
6. Swarms of flying moths can be seen at any time of the day in hot rooms and in conditions of overcrowding with mutual stimulation.

(C) *Distribution of moths in temperature gradients.*

The effect of temperature on the distribution of moths was first noted in a warehouse room filled with deteriorating English oats, with two hot spots, which extended throughout about a quarter of the room. The emergence of moths in this room was a month earlier than in similar rooms, where grain was not heating. Distribution of moths in relation to temperature and light gradients was worked out on two days (8.vi.43 and 24.vi.43), but these observations could not be continued, as the room was cleared of oats. Moths were counted on sample ceiling areas only, as generally the total number of moths on ceilings represented 60–70% of the whole population. Light readings were taken on the same ceiling areas, and temperature and humidity readings immediately beneath them. On the first day the highest grain temperature was 38.9° C. and the second highest, probably the centre of another hot spot, was

27.5° C. Away from the heating oats the grain temperature varied between 15.9 and 16.5° C. This had an effect on air temperature producing a gradient of 19.3–22° C. (70–66% R.H.). The room was dark and the light intensity varied between 0.065 and 0.0003 F.C., with only one reading of 0.144 F.C. above this range. The total number of recorded moths was 414, the correlation coefficient between the moth numbers and temperature was high, $r = +0.6499$, $n = 38$, $p < 0.01$. There was no significant correlation between the intensity of light and the numbers of moths until the effect of temperature was eliminated when in a partial correlation coefficient r was -0.4145 , $n = 38$, $p < 0.01$. Thus it is evident that air temperature gradients of 3° C. are effective in producing aggregations of moths in the warmer parts of the room, and that the reaction to temperature overrides the effect of light of very low intensities. On a later date, when the room was two-thirds cleared of oats, the air temperature gradient was very small and varied between 17.9° and 18.5° C. (R.H. 52.54–6%), and

TABLE 11.

Date	Heated end of the box		Colder end of the box	
	T° on glass roof, ° C.	On grain floor, ° C.	On glass roof, ° C.	On grain floor, ° C.
23.ii.44, 11 p.m.	20.8	19.75	18.25	17.5
24.ii.44, 11 p.m.	19.6	18.2	17.5	16.0
3.30 p.m.	19.0	19.8	17.0	18.0
25.ii.44, 2 p.m.	21.5	19.5	18.2	17.5
28.ii.44, 11 p.m.	19.0	18.0	16.0	15.5
2 p.m.	20.4	19.5	18.0	16.5
29.ii.44, 2 p.m.	20.6	20.0	18.0	17.0

there was no correlation between this gradient and moth distribution. As some of the oats were removed, light intensity in the room was higher and very uniform, except in one dark corner of 0.008–0.0045 F.C., where moths were abundant. Elsewhere, the light gradient varied between 0.3 and 0.025 F.C. with one exception above this range, and this slight gradient had no apparent effect on the distribution of moths.

Laboratory data. Some simple experiments were carried out as a check on the apparent effect of small temperature gradients on the distribution of moths. The apparatus consisted of two wooden boxes, one 36 in. long, 9 in. wide and 8.5 in. high, and the other 72 in. long, 10.5 in. wide and 10.5 in. high, with glass plates on top and a blackened glass plate at one end, which was heated by a 60-watt electric bulb. To ensure uniform heating, this glass plate was covered with a sheet of perforated zinc. The floor of each box was covered with grain which provided an oviposition site for the females and, to a certain extent, controlled humidity. The whole apparatus, except the end plate, was insulated with thick felt and was in complete darkness. Thermometers were fixed on the glass roof and others were laid on grain. There were considerable difficulties in these experiments, for although the boxes were insulated the temperature in them fluctuated with the changes in the laboratory temperature, there were vertical as well as horizontal gradients, and the horizontal gradient fell off steeply, leaving two-thirds of the box at a uniform temperature. The following is an example of the variations in the extremes of temperature in one of the boxes (Table 11).

(1) *Thermotaxis in heat gradients.* Five sets of experiments were carried out in which the boxes were treated as "choice chambers" and the numbers of moths in the warmer and colder halves compared. When the readings were taken, the moths were exposed to light; some were disturbed, took to wing, and were not included in the counts. The results of these observations are given in Table 12.

TABLE 12.

Distribution of moths in warmer and colder halves of the heat box. ¹

Set	No. of moths	Dates of exp.	Extremes of temp. in ° C. in the experiment, ° C.	Extreme temp. gradient in any one reading, ° C.	No. of moths recorded, Warm Cold half half		Same in %	
I	30	25.i.-4.ii.44	24.5-15.5	8	382	166	69.7	30.3
II	16	20-24.vi.44	24 -18	4.5	141	20	87.5	12.5
III	25	31.vii.-3.viii.44	24.5-21	3.5	97	85	53.0	47
IV	26	23-29.ii.44	21.5-15.5	3.6	114	44	72.2	27.8
V	25	7-9.ii.44	23.4-15.8	4.8	70	25	73.6	26.4

On the whole, the tendency to move to the warmer part of the apparatus is well pronounced, except in Set III, and the temperature gradient is small, approximating to that encountered in warehouse conditions. The moths reacted to the highest temperature of the gradient independently of whether it was 24.5° C. or 20° C. Deal (1941), in analysing the temperature preferendum of a number of insects, concluded that while the insects had a definite temperature preference, the preference was for a fairly wide range. This is also clearly true for *E. chutella* moths.

TABLE 13.

Distribution of antennaless moths in heat gradients.

Set	No. of moths		Extremes of temperature in experiment, ° C.	Extreme t° range in any one reading, ° C.	No. of moths recorded in		
					Warm part	Middle	Colder part
I	10 ♂	10 ♀	15.7-23.2	5.6	112 (50.6%)	—	109 (49.4%)
II	17 ♀	—	18 -23	4.0	37 (48.6%)	9	39 (51.4%)

No detailed analysis was made of the responses of moths to temperature gradients, but both the laboratory and the warehouse data point to a positive thermotactic reaction. This reaction usually becomes more clearly expressed in older moths, as initially the distribution of the males is partly dependent on that of the young "calling" females (fig. 3).

(2) *Distribution of antennaless moths.* In two further sets of similar experiments the antennae of the moths were amputated. Antennaless moths do not fly, but they can walk and hop about actively. The distribution of these moths in the two halves of the box was uniform, indicating that the antennae are essential for this reaction. Wigglesworth and Gillett (1934) have found that the thermal reaction disappeared in *Rhodnius prolixus* Stål when the antennae were removed.

(3) In two other sets of experiments the heated end of the box was exposed to daylight and in such conditions the distribution of the moths in the two halves of the apparatus was again almost uniform. Much more work would be needed to estimate the relative importance of heat and light in the distribution of the moths, although the warehouse data suggest that at low light intensities positive thermotaxis overrides negative phototaxis. Set II of these experiments was continued until all the moths were dead; 12 out of 15 died in the lighter warmer part of the box. This drift of physiologically older moths to light has already been described (see distribution of moths in light), and it still further complicates the analysis of the distribution of moths under natural conditions (Table 14).

TABLE 14.

Distribution of moths in a box with the heated end exposed to daylight.

Set	No. of moths	Extremes of temperature in experiment, ° C.	Extreme t° range in any one reading, ° C.	No. of moths recorded in		
				Warm light part	Middle	Colder dark part
I	21	16.50-25.5	8	119 (52.4%)	—	108 (47.6%)
II	15	16.5-24.5	6	76 (52%)	21	70 (48%)
		No. of dead moths in Set II			12	1

(4) *Kinetic effect of heat.* Experiments on thermokinesis produced by gradual rise and fall in temperature (within the range of 15-30° C.) will be described in a later paper giving a fuller account of the periodicity of activity of moths. These experiments are still in progress and at the moment it will be sufficient to say that (a) gradual rise and fall in temperature induces movements, even in high light intensities, which immobilise the moths; (b) this kinesis is not strongly expressed; although moths walk and hop, they rarely fly; (c) sharp temperature changes induce rapid movements, gradual changes may have no effect, and it appears that below 25° C. adaptation to thermal changes is rapid.

Summary of the reactions of moths to temperature gradients.

1. Both warehouse and laboratory data show that the moths are positively thermotactic and that they react to temperature differences of 3° C.
2. Warehouse observations suggest that thermal responses override negative phototaxis, at least at low light intensities.
3. There are indications that thermo-receptors are located in the antennae.
4. Preliminary experiments indicate that sharp temperature changes (within 15-30° C.) induce movements and that slow changes may have no effect, at least at high light intensities at which the moths are inactive.

(D) *Reactions of moths to air currents.*

An attempt in an empty storage room to correlate the distribution of moths with air currents proved inconclusive. The numbers of moths, light intensities, and readings of air currents, were recorded for 115 areas on 14.vii.44. The wind readings were unsatisfactory; in 78 areas no readings were obtainable and in the 37 where a reading was obtained (some movement of the vanes in 1 min.) there was much difference according to the exact spot where the

instrument was held, and also to varying wind intensities outside the windows (which were open). The moth numbers were significantly negatively correlated with light (a) in the room as a whole, (b) in windless (78) and draughty (37) areas separately, (c) in the draughty areas, eliminating the effect of wind (partial correlation).

The correlations between moth numbers and wind, (a) in the room as a whole, and (b) in the draughty areas only, were negative but not significant, and (c) when the effect of light on (b) was eliminated, the result was still a non-significant negative correlation. Light and wind were positively correlated, but this figure too was not significant. Table 15 gives a summary of the

TABLE 15.

Relation of moth numbers to wind and light in areas where the wind-reading was greater than 0.

No. of areas	No. of moths		Wind reading		Light reading	
	Range	Mean	Range	Mean	Range	Mean
7	9-24	12.3	2-31	17.3	0.03- 1.93	0.49
7	6- 7	6.9	3-39	13.3	0.1 - 1.0	0.46
9	3- 5	4.0	2-37	12.3	0.07- 0.35	0.28
5	1- 2	1.6	2-11	7.6	0.3 - 3.5	1.40
9	0	—	2-94	31.0	0.3 -14.0	5.14
37			Windless areas reading 0			
22	9-25	13.3		—	0.035- 5.00	0.48
16	6- 8	6.6		—	0.030- 8.50	0.59
16	3- 5	3.9		—	0.135- 2.50	0.58
17	1- 2	1.6		—	0.059-18.00	3.20
7	0	—		—	0.70 -35.00	9.50
78						

results, showing the correlation with light, more marked in the windless areas. It is just possible that moderate wind immobilises moths while stronger winds drive them away. There is little doubt, from general observation in the warehouse, that moths avoid areas of high light intensity and strong draughts near windows.

II. OBSERVATIONS ON THE BEHAVIOUR OF LARVAE.

Behaviour of *Ephestia elutella* larvae on bulk grain.

In the warehouse the egg incubation and the feeding larval stage together last 60-70 days at the average grain temperature of 16.9° C., average air temperature of 15.7° C. and R.H. of the air 63.6%. While feeding, some of the larvae moult four and some five times. The fully grown larvae leave the food and wander on to the walls and ceiling. This wandering stage lasts 1-3 days, and in a few exceptional cases as long as 4 weeks (see Richards and Waloff). The larvae then spin up in crevices where they spend the winter as resting larvae. A very small number of larvae pupate immediately and produce the second annual generation.

This section is divided into two parts : (A) the distribution of feeding larvae in grain, (B) observations on the distribution of wandering larvae.

(A) *Distribution of feeding larvae.*

The presence of *E. elutella* larvae in grain is easy to detect as the larvae feed on the embryo only, scooping it out neatly and often exposing the groove of the under-surface. The feeding habits of larvae in grain were first described by Dendy and Elkington (1919). Moreover the larvae produce webbing with frass adhering to it, and this also indicates the presence of *E. elutella* in grain. In the warehouse, the estimation of the numbers of damaged grains in samples of 500 taken from different depths gives a clear picture of the distribution of larvae throughout the feeding stage. The greatest number of larvae, and hence the greatest amounts of damage, are always found in the upper 30 cm. of grain, but penetration down to 100 cm. and even lower is not uncommon. Table 16 provides an example of this, where only 3 samples out of the 13 drawn below 100 cm. were free from damage.

TABLE 16.

Per cent. damage of warehouse grain at different depths.

	Depth at which samples were taken, cm.	% of grains with embryos eaten out (from sample of 500 grains).
Samples from 30 areas . . .	Surface	15.5
" " " " " "	8	11.9
" " " " " "	25	5.4
" " " " " "	50	1.0
" " " " " "	75	0.8
" " " " " "	100	0.7
" " 13 areas . . .	Below 100 cm.	0.36

Laboratory data.

(a) *Distribution in grain and the age of larvae.*

Originally the apparatus used consisted of glass cylinders 13.5 cm. in diameter and 20 or 30 cm. high. These cylinders could hold 2-2.5 kg. of grain. The grain used was Manitoba No. 1 wheat conditioned to 70% R.H. at 25° C. Freshly hatched larvae were placed on top of the grain which was covered with muslin, the cylinders were wrapped in black paper and kept at 25° C. 70% R.H., for the required length of time. The cylinders were then marked in centimetres on the outside and the grain spooned out and examined for larvae. The larval stage under these conditions lasts 36 days on the average. Table 17 provides the summary of these data. It can be seen that the penetration of the larvae into grain is gradual, and in the upper 20 cm. of grain is greatest at 3 weeks. After 3 weeks (at 25° C.) the larvae begin to drift upwards and finally leave the food. As not all larvae develop at the same rate, this drift is gradual, and the smaller larvae are found at greater depths than the feeding last instar larvae. This was clearly seen when 4-week-old larvae from different depths were weighed, i.e. the weights of the larvae decreased progressively with the depth down to 19 cm. (see Table 17 and fig. 4).

The initial drift of the larvae downwards was also seen in warehouse bulk grain. The warehouse samples were taken by plunging metal tubes 10 cm. wide and 36 cm. long into the grain and then subdividing the grain into smaller

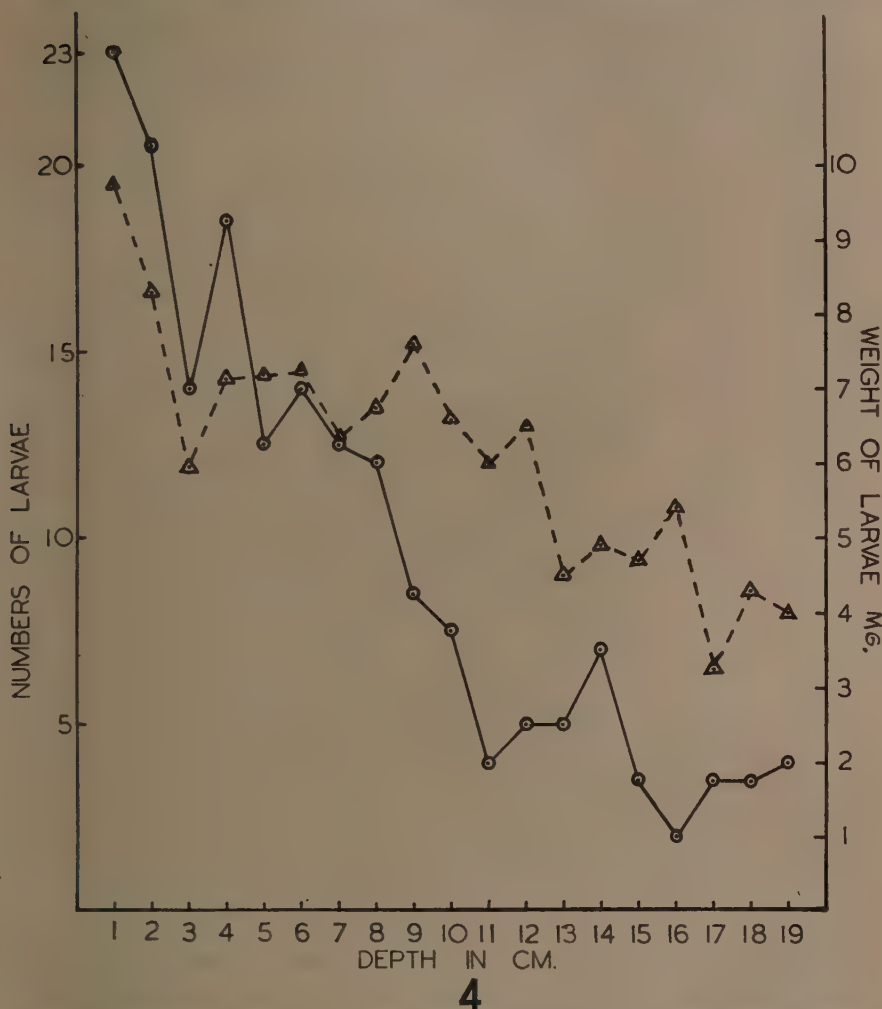


FIG. 4.—Numbers of larvae (○—○) and weights of larvae (△—△) in mg. plotted against depth in cm. at which they were found in the 20-cm. cylinder of grain, four weeks old, at 25° C. 70% R.H.

samples by running it out into 1-cm.-deep containers. Samples taken on 4.viii.42 show the maximum damage, and the maximum number of larvae in the upper 5 cm., whereas those taken on 12.viii.42 show the two maxima at 11 cm. (see fig. 5). The warehouse data, however, can never present an equally coherent picture of the downward and upward movements of the larvae, as

the infestations are progressive, depending on the prolonged period of moth emergence and oviposition, lasting about 14 weeks. Further experiments on the distribution of larvae to greater depths of grain were made in long glass or metal towers 7.5 or 10 cm. in diameter, 60 or 120 cm. long. The towers were set up in 25° C. 70% R.H., and grain conditioned to this humidity was used. As before, just-hatched larvae were placed on top of the towers, and the grain was subdivided into smaller samples by sliding it into 5-cm.-deep containers of 10-cm.

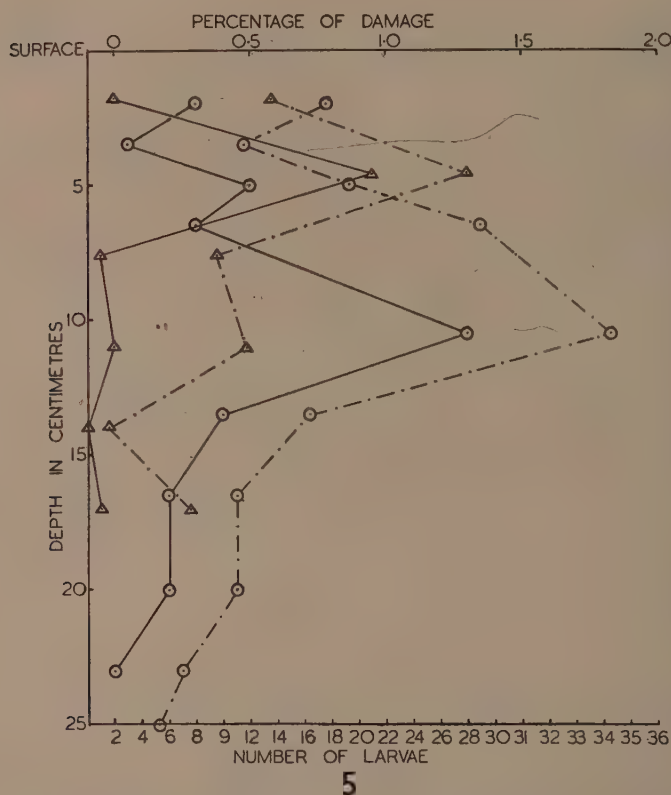


FIG. 5.—Numbers of larvae and percentage of damaged embryos found in bulk grain in granary plotted against depth in cm. Larvae: Δ—Δ, 4.viii.; ●—●, 12.viii. Percentage embryo damage: Δ- - Δ, 4.viii.; ●- - ●, 12.viii.

diameter, after required intervals of time. In the experiments with one or two week-old larvae the smaller samples so obtained were kept at 25° C. for another fortnight, until the larvae were large enough for counting to be easy (see Table 18). The results obtained from these larger towers do not show larval movements so clearly in the upper 20–30 cm.; on the other hand, they show the gradual penetration of larvae into the greater depths of grain with time, from the beginning of an infestation, and also that even the first instar larvae sometimes

wander down to the depth of 50 cm. This has also been encountered in deep samples brought back from the warehouse.

(b) Possible causes for the movements of larvae in grain.

(1) *Nature of food.* On hatching the first instar larvae proceed to find suitable grains. As can be seen in Table 18, they may even penetrate down to 50 cm. before finding their way into an embryo. The pericarp of the grain is often nibbled before the larvae find the softer embryo. Reh (1907) speaks of the preference of *E. elutella* larvae for softer foods. The first and second

TABLE 18.

Distribution of larvae with age in long towers.

Depth of grain, cm.	Age of larvae									
	1 week		2 weeks		3 weeks		4 weeks		5 weeks	
1- 5 . . .	132	46	36	26	21	61	32	25	37	
5- 10 . . .	3	7	2	21	13	41	8	26	24	
10- 15 . . .	0	0	0	3	5	3	7	5	7	
15- 20 . . .	1	1	1	0	0	1	1	3	0	
20- 25 . . .	0	0	1	2	6	3	2	0	0	
25- 30 . . .	0	0	3	5	3	0	0	5	3	
30- 35 . . .	1	0	0	0	2	2	1	1	0	
35- 40 . . .	0	0	4	0	1	0	1	3	0	
40- 45 . . .	0	0	3	1	5	0	1	1	1	
45- 50 . . .	0	1	5	0	0	0	0	5	0	
50- 55 . . .	0	0	0	2	4	0	4	5	0	
55- 60 . . .	0	0	0	0	4	0	11	4	0	
60- 65 . . .						0			1	
65- 70 . . .						0			0	
70- 80 . . .						0			1	
80- 90 . . .						0			0	
90-100 . . .						0			1	
100-120 . . .						0			0	
Total . . .	137	55	55	60	64	111	68	83	75	
Initial no. larvae .	150	100	100	100	100	125	100	100	100	
% survival . . .	91.2	55	55	60	64	88.8	68	83	75	

instars are usually passed inside the grain, the larva lying curled up inside the embryo. Its presence can be detected by a small puncture at the tip of the embryo, through which frass can be extruded. The larvae, however, leave the embryos to moult, and in many laboratory observations were seen to return to the same grains after the first moult. When a larva reaches the third instar, or by the end of the third instar, it is too large to fit inside the grain embryo, and the rest of the larval feeding stage is passed outside the grains. As one larva requires about 48 embryos to complete its development, its food habits alone necessitate wandering and the spreading of larval population. It is only in the hard wheats of Manitoba type that the embryo alone is attacked; in softer English wheats some of the endosperm is also eaten. The distribution of *E. elutella* in other cereals is probably similar to that in grain. In unpolished rice each larva eats 96 embryos, on the average, and the larval population probably spreads even more extensively. The distribution of larvae in a tower of English oats was similar to that in Manitoba wheat. On the other hand,

in other types of foods, such as peanuts, beans, cacao beans, the whole of the larval feeding stage is passed inside one bean and the wandering of the feeding larvae cannot be so extensive. In finely ground foods, such as whole-wheat flour, or wheat embryo, the distribution of larvae is again restricted; in the two experiments with towers of whole-wheat flour the larvae penetrated down to 5 cm. in one tower and to 10 cm. in the other. Similarly, in towers where layers of grain alternated with whole-wheat flour or grain embryo, the finely ground foods restricted larval distribution.

These experiments are summarised in Table 19.

TABLE 19.

4-week towers, with whole-wheat flour.			4-week tower, grain alternating with whole-wheat flour.		18-day small tower, grain alternating with wheat-germ.	
Depth, cm.	No. of larvae.		No. of larvae.		Depth	No. of larvae
1- 5 . . .	37	59	Grain . . .	38	1-cm. grain . . .	108
5-10 . . .	1	0	" . . .	24	2-cm. wheat-germ . . .	63
10-15 . . .	0	0	Flour . . .	1	3-cm. " . . .	11
15-20 . . .	0	0	Grain . . .	0	4-cm. grain . . .	0
20-25 . . .	0	0	Flour . . .	0	5-cm. " . . .	0
25-30 . . .	0	0	" . . .	0	6-cm. " . . .	0
30-35 . . .	0	0	Grain . . .	0	7-cm. " . . .	0
35-40 . . .	0	0	" . . .	0	8-cm. " . . .	0
40-45 . . .	0	0	" . . .	0	9-cm. " . . .	0
45-50 . . .	0	0	" . . .	0	10-cm. wheat-germ . . .	0
50-55 . . .	0	0	" . . .	0	11-cm. " . . .	0
55-60 . . .	0	0	" . . .	0	12-20-cm. grain . . .	0
Total . . .	38	59		63		182
Initial no. of larvae . . .	100	100		75		200
% . . .	38	59		84		91

The experiment with wheat germ was examined after 18 days, as the development of larvae on this food is very rapid.

The restricted wandering of larvae in finely ground foods and in foods such as cacao beans may result from several causes: (1) the larvae are surrounded by uniform food material, they eat the whole of it, and do not select a part, as in hard wheats, (2) the mechanical texture of finely ground foods may limit wandering, (3) the whole larval body, including the long dorsal setae which are nearly as long as the body is wide, is in close contact with the food. Grain, on the other hand, is of a fairly loose texture and wandering in it may be due to thigmokinesis. In wheat, the tactile stimuli must be fully satisfied in the first and second instar larvae, but when the larvae become too large to fit inside the embryos, the lack of total contact due to the small gaps between the grains probably causes greater activity and wandering. Feeding larvae will move about actively in empty glass towers but become much less active in towers filled with glass beads, where they can still move about freely, but much of their body is in contact with solid surfaces.

(2) *Weak positively geotactic reaction of the feeding larvae.* It is suggested that the downward movements of the larvae in grain can be ascribed to a weakly expressed positively geotactic reaction. It is probable that this stimulus

is operative only when the contact stimuli are at least partly satisfied. Thus, in empty glass towers the feeding larvae tend to wander upwards, whereas in those filled with glass beads the movement tends to be a downward one. It is probable that there is an interaction between positive geotaxis and thigmokinesis. Contact stimuli appear to induce downward movement, unless they are received on all sides, when the larva becomes immobile.

When single freshly hatched larvae were placed on top of grain-containing cylinders 22 cm. in length and 6 cm. in diameter and left for 2 or 3 weeks, many of the larvae penetrated to much greater depths than their food requirements would have necessitated. These results are summarised in Table 20.

TABLE 20. -

Single larvae placed on top of grain cylinders (6 cm. diam.), 22 cm. long.

Depth of grain to which single larvae penetrated, cm.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Number of single 2-week-old larvae (total no. of experiments = 60) .	0	2	4	4	6	3	2	3	7	5	4	4	2	0	4	2	1	2	0	3	1	1
Number of single 3-week-old larvae (total no. of experiments = 20) .	0	2	1	1	2	2	1	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1

Further experiments which suggest the positively geotactic reaction included: (i) starting larval populations half-way down grain towers and noting their subsequent distribution, (ii) noting the distribution of larval populations started from the top and from the bottom of towers, (iii) noting the distribution of larvae in vertical and horizontal towers.

(i) *Distribution of larval populations started half-way down a tower.*

Four towers, 10 cm. in diameter, 3 of them 60 cm. long and one 100 cm. long, were set up in which the freshly hatched larvae were placed half-way down. As in all experiments, grain conditioned to 70% R.H. was used, and the towers were kept in a constant temperature room running at 25° C. 70% R.H. After 3 weeks the grain was subdivided into sections and the distribution of the larvae was noted. Another similar 60-cm. long tower was kept for four weeks. The results of larval distribution obtained from these towers are given in Table 21.

The downward drift of larvae in the three-week-old towers was quite clear; out of the total of 422 surviving larvae 116 moved upwards and 306 downwards, i.e. 27.5% moved up and 72.5% moved down. More larvae were found in the upper half of the four-week-old tower, but this may be due to a fairly early upward drift of last instar larvae.

(ii) *Distribution of larval populations started at the top and bottom of towers.*

Six 60-cm.-long grain towers were set up, in three of which the larval populations were started at the bottom and in the other three control towers from the top. The distribution of the larvae was estimated in the usual way after 24 days. The distribution of the larvae started from the bottom of towers was not so extensive as of those started from the top, and in the two experiments where percentage damage at different depths was calculated, it was also more

TABLE 21.

Distribution of larval populations started half-way down a tower.

Depth, cm.	Age of larval population				
	3 weeks				4 weeks
	Initial no. of larvae				Initial no. of larvae
	100	150	200	150	100
1- 5	0	0	28	0	17
5- 10	0	0	11	0	12
10- 15	0	0	6	1	8
15- 20	4	0	6	0	5
20- 25	3	2	3	0	1
25- 30	10	10	3	2	2
30- 35	18	71	4	3	3
35- 40	3	24	6	0	1
40- 45	6	4	16	10	1
45- 50	5	3	17	14	5
50- 55	1	7	15	42	7
55- 60	7	3	21	22	16
60- 65				4	
65- 70				0	
70- 75				0	
75- 80				2	
80- 85				3	
85- 90				1	
90- 95				0	
95-100				0	
Total	57	124	136	104	78
% of original no.	57	83	68	69	78
No. in upper half.	17	12	57	30	45
No. in lower half.	40	112	79	74	33

TABLE 22.

Distribution of larval populations started at the top and bottom of towers, after 24 days.

Depth, cm.	Exp. 1				Exp. 2				Exp. 3	
	Started at top		Started at bottom		Started at top		Started at bottom		Started at top	Started at bottom
	No. of larvae	% damage *	No. of larvae	% damage *	No. of larvae	% damage	No. of larvae	% damage	No. of larvae	No. of larvae
1- 5	33	36	0	0	42	36	0	0	11	0
5-10	20	30	0	0	19	28	0	0	29	0
10-15	13	25.6	0	0	12	14	0	0	3	0
15-20	10	5	0	0	3	6	0	0	1	1
20-25	5	4	0	0	5	4	0	0	1	0
25-30	6	1.8	0	0.1	1	0.5	0	0	0	1
30-35	2	2	0	0.1	3	1.2	0	0	2	0
35-40	2	0.2	1	0.5	2	0.5	0	0	4	0
40-45	5	0.2	3	3.5	1	0.1	0	0.5	0	0
45-50	3	0.3	15	16	0	0.3	1	6	1	14
50-55	4	1.5	31	34	2	0.5	59	40.5	1	18
55-60	2	0.5	57	45.5	2	1.5	56	49	0	21
Total	105	—	107	—	92	—	116	—	53	55
Initial no.	150	—	150	—	150	—	150	—	100	100
% survival	70	—	71.3	—	61.3	—	77	—	53	55

* Samples of 300 grains.

widespread in the towers where populations were started at the tops of towers. These results are summarised in Table 22.

Apparently the weight of grain in experiments where larval populations were started half-way down and at the bottom of towers had no effect, as the percentage survival of larvae did not differ from that in control towers. A control experiment was also set up in which 5.8 kg. weight was placed on top of a cylinder of grain with larvae, and again in this case the percentage survival was high (85%) and the distribution of larvae was normal.

TABLE 23.
Distribution of larvae in vertical and horizontal towers.

Depth, cm.	Exp. 1		Exp. 2		Exp. 3			
	Grain towers, 10 cm. diameter, 60 cm. long		Grain towers, 10 cm. diameter, 120 cm. long		Grain towers 7.5 cm. diameter, 120 cm. long			
	Vertical tower. No. of larvae	Horizontal tower. No. of larvae	Vertical tower. No. of larvae	Horizontal tower. No. of larvae	Vertical tower. No. of larvae	Horizontal tower. No. of larvae	Vertical tower. % damage to grain *	Horizontal tower. % damage to grain *
1-5	24	41	8	13	72	35	40.5	31
5-10	18	17	9	31	25	44	26	26.5
10-15	4	2	21	18	21	24	17.5	16.5
15-20	3	1	22	9	5	13	3.5	4.5
20-25	0	0	1	0	9	7	2.3	2.6
25-30	4	1	1	0	2	2	0.8	1.3
30-35	4	0	2	0	0	0	0.15	0.15
35-40	2	0	3	1	0	0	0	0
40-45	0	0	0	0	1	0	0.3	0
45-50	1	1	0	0	1	0	1.0	0
50-55	3	2	1	0	0	0	1.0	0
55-60	4	3	2	0	0	0	0.3	0
60-65	—	—	1	1	0	0	0.3	0
65-70	—	—	0	0	1	0	0.6	0
70-75	—	—	0	0	0	0	0	0
75-80	—	—	2	1	0	0	0	0
80-85	—	—	1	0	0	0	0	0
85-90	—	—	0	0	0	0	0	0
90-95	—	—	1	0	0	0	0.3	0
95-100	—	—	0	0	0	0	0.3	0
100-105	—	—	0	0	0	0	0	0
105-110	—	—	2	0	1	0	1.0	0
110-115	—	—	1	0	0	0	0	0
115-120	—	—	0	0	0	0	0	0
Total larvae	66	68	77	75	138	125	—	—
Initial no.	100	100	100	100	150	150	—	—
% survival	66	68	77	75	92	83	—	—
No. of larvae in infested half of tower	53	62	69	73	136	125	—	—
No. of larvae in distant half	13	6	8	2	2	0	—	—

* Samples of 300 grains.

(iii) *Distribution of larvae in vertical and horizontal towers.*

Six towers were set up in the usual way—three of them were placed vertically and three horizontally. After a period of four weeks the grain in the towers was subdivided into sections and examined for larval distribution. In one set of towers the percentage of damage to grain in each section was also worked out. As can be seen in Table 23, larval populations are more widespread in vertical towers than in the horizontal ones, and whereas grains damaged by larvae were found at the depth of 110 cm., they extended along the length of only 30 cm. in the horizontal tower (Expt. 3). Although the data from these experiments

are not as convincing as from towers with larval populations started half-way down, they again point to the tendency of larvae to move down rather than horizontally.

The application of the χ^2 test to these experiments showed the results to be significant:—

Number of larvae in	Infested half of tower	Distant half of tower
Vertical towers	258	23
Horizontal towers	260	8

$$\chi^2 = 6.96, p < 0.01.$$

Warehouse observations.

The distribution of larvae and hence of damage in warehouse bulk grain is patchy. In 1943 the amount of oviposition and, later, the degree of damage down to 100 cm. was determined on 30 sample areas (see Richards and Waloff). The correlation coefficient between the numbers of eggs laid on sample areas and the amount of damage caused by larvae was significant, $r = +0.4423$, $n = 28$, $p = 0.02-0.01$, indicating that the feeding larvae do not wander far from oviposition sites and that the larval population tends to spread downwards, rather than horizontally.

It is difficult to understand the origin of a positively geotactic reaction in the feeding larvae when they lived out of doors, but this tendency to move downwards undoubtedly exists. The most convincing evidence for it has been obtained from the examination of towers containing single larvae, and from the distribution of larval populations initially placed half-way down the towers. The upward drift of feeding larvae in empty glass towers, and movements down in glass towers filled with glass beads, indicate that this reaction is not independent of thigmokinesis.

(3) *Effect of crowding on penetration into bulk grain.* The relation between the number of larvae moving downwards and the density of larval populations was first seen in warehouse samples. An instance of this is provided by two sets of samples drawn on the same day (12.viii.42) from bulk grain. The numbers of larvae found in the surface and deep samples are given below.

First set of samples			Second set of samples		
Depth of sample, cm.	Weight, g.	No. of larvae	Depth of sample, cm.	Weight, g.	No. of larvae
Surface	148.9	30 larvae (14 eggs)	Surface	136.0	170
15	97.9	0	15	107.7	3
25	107.4	0	25	111.6	2
50	110.8	1	50	113.8	4

The effect of crowding on penetration was analysed in laboratory towers, and the results of two sets of experiments are given below.

Set I. Two 60-cm.-long towers 7.5 cm. in diameter were set up in the usual way. Three hundred hatched larvae were put in one and 150 in the other. After four weeks the towers were subdivided into sections, and the number of larvae and percentage damage to grain samples were determined (Table 24).

Set II. Nine 60-cm.-long towers (10 cm. in diameter) full of grain were set up and analysed in the usual way after four weeks; 4 were with 50 freshly hatched larvae, 3 with 100 larvae in each and 2 with 200 larvae in each. The results of these experiments are given in Table 25.

TABLE 24.

Effect of larval density on penetration into grain.

Depth, cm.	Initial no. of larvae			
	150		300	
	No. of larvae	% of damaged grains (from samples of 300)	No. of larvae	% of damaged grains (from samples of 300)
1-5	20	29	53	48
5-10	28	20.8	45	51
10-15	41	25	54	50
15-20	24	10	57	35
20-25	6	6.6	17	15
25-30	2	2.8	2	8
30-35	1	0.8	2	5
35-40	0	1.0	3	4
40-45	0	0.6	4	5
45-50	1	0.8	6	4
50-55	0	1.2	0	5
55-60	0	0.8	6	5
Total	123	—	249	—
% survival	82	—	83	—
No. of larvae in upper half	121	—	228	—
No. of larvae in lower half	2	—	21	—
Av. % damage in upper half	15.7	—	34.5	—
Av. % damage in lower half	0.86	—	4.66	—

TABLE 25.

Effect of larval density on penetration into grain.

Depth, cm.	Initial number of larvae								
	50				100		200		
	Number per sample								
1- 5	7	10	25	11	32	25	15	21	26
5-10	14	5	7	6	8	20	20	15	16
10-15	7	5	4	1	7	5	5	17	11
15-20	1	2	2	1	1	3	4	16	8
20-25	0	5	0	2	2	0	2	6	13
25-30	1	2	1	5	0	5	0	4	4
30-35	0	0	0	3	1	1	0	3	2
35-40	2	0	0	4	1	3	5	3	4
40-45	0	1	0	4	1	1	2	6	8
45-50	0	0	0	0	0	5	5	6	5
50-55	0	0	5	3	4	5	1	11	3
55-60	4	1	2	3	11	4	7	28	8
Total	36	31	46	43	68	83	72	136	108
% survival	72	62	92	86	68	83	72	68	54
No. in upper half	30	29	39	30	50	64	52	79	78
No. in lower half	6	2	7	17	18	19	20	57	30
Total in upper half	126 79.7%				166 74.4%		157 64.3%		
Total in lower half	32 20.3%				57 25.6%		87 35.7%		

Applying the χ^2 test to the difference in larval distribution in the upper and lower halves of towers, with 50 and 100 larvae, shows that this difference is not significant, *i.e.* $\chi^2 = 1.4512$, $p = < 0.5$. However, the difference in larval distribution in the two halves of towers with initial numbers of 50 larvae and 200 larvae and also of 100 larvae and 200 larvae is significant; in the first case $\chi^2 = 10.917$, $p < 0.01$ and in the second $\chi^2 = 5.5667$, $p > 0.01 < 0.02$.

These results suggest that at high larval concentrations the downward drift of larvae is greater than would be accounted for by the density of larval populations at the surface. Such high densities have been encountered in warehouse samples, but as larvae have been found at the depth of 50 cm. and 100 cm. when the density was low, high larval concentrations alone cannot be responsible for the movement into the deeper grain layers. It is thought that in crowded conditions larvae activate one another and that this activation results in greater movement, which tends to be a downward one.

(4) *The possible effect of water content of grain and of relative humidity on larval distribution.* There are no other substances stored in such large homogeneous masses as bulk grain, and it is difficult to imagine larval development proceeding in a more uniform environment. The thermal conductivity of wheat is low (Oxley 1944) and hence the temperature variations, apart from those in the superficial layer, are slight. During the whole period of larval development in 1943 (29.vi.–2.ix.) the mean temperature of bulk grain was 17.6° C. with the maximum of 19.6° C. and minimum of 16.1° C. In 1944 the average temperature for this period was 17.8° C., the maximum 23.3° C. and minimum 16.1° C. The changes in temperature were slow and gradual, not exceeding 2° C. for a period of a whole week.

The water content of the grain is also uniform, the upper layers usually becoming slightly moister on prolonged storage. The relative humidity of the air in the intergranular spaces is determined by the water content of the grain, and the gradients are slight. Examples of variations of the percentage water content of grain drawn on 4.ii.43, from different depths of the studied stored bulk, are given below.

Depth of samples		5 cm.	15 cm.	25 cm.	50 cm.	100 cm.
% Water content of grain.	Site 1	15.9	14.6	14.0	13.9	14.0
	" 2	15.4	14.3	14.1	13.9	13.9
	" 3	15.4	14.6	13.9	13.8	14.1

The extremes of 15.9% and 13.8% water content represent a range of relative humidity of about 67–76%.

Preliminary laboratory experiments have shown that, on the whole, the feeding larvae show a preference for grain of higher water content. The effect may be one of humidity or of the softness of food of higher water content, but in either case it would tend to restrict the larvae to the upper layers of wheat. Thus it appears that the spreading of larval populations in the bulks studied must be independent of the water content of the wheat, but to be due to the feeding habits of the larvae and to other patterns of behaviour, such as thigmokinesis and positive geotaxis and the activation of crowded larval populations.

It may be added here that although in the laboratory experiments wandering larvae, which have ceased feeding, show a preference for lower humidities, in the warehouse they move upwards in grain towards the upper layer of higher humidity, before leaving the food altogether. Moreover, they wander in rooms the air humidity of which, at that time of the year, is generally higher than that in bulk grain.

Thus, it is considered that although humidity reactions may exist in the feeding and in the wandering larvae, they are inhibited by other factors, and are of very little importance in determining the distribution of larvae.

Summary of the results on larval distribution in bulk grain.

1. The laboratory experiments on the distribution of larvae were suggested by observations in the warehouse.

2. Most of the larvae pass the feeding stage in the upper 30 cm. of grain, but penetration to 100 cm. and lower is not uncommon.

3. The spreading of infestations throughout the grain is gradual. Most, though not all, larvae of first and second instar live inside the embryos in the upper 20 cm. of grain. However, first instar larvae, occasionally, have been found at the depth of 50 cm.

4. Generally there is a slight shift of the larval population downwards as the infestation progresses in time. Later, the feeding last instar larvae move upwards and finally leave the grain.

5. The distribution of larvae in grain is attributed to the combination of the following factors:—

(a) Each larva requires about 48 grain embryos to complete its development, and this feeding habit in itself necessitates wandering.

(b) It is suggested that larval movements are induced by a combination of thigmokinesis and positive geotaxis.

(c) Crowding of larvae results in a more pronounced downward drift. This downward movement is not directly proportional to the initial numbers at the surface, and it is thought that mutual stimulation in crowded conditions leads to greater activity which is expressed in movements downwards.

(d) Under normal conditions of storage of bulk grain, it is thought that the effect of water content of wheat on larval distribution is less important than the other factors.

(B) Observations on wandering larvae.

(1) *Negative geotaxis of wandering larvae.* The fully grown larvae leave the grain and wander on walls and ceiling, leaving a silk trail as they move. Experiments conducted by Dr. J. Blacklocks in this laboratory have shown that the larvae do not follow their own or other silk trails. Towards the end of the wandering period, which for the whole larval population lasts approximately six weeks, sheets of silk may be formed on tops of grain cones, on walls and on ceiling. The average length of the wandering stage for each larva worked out at 56 hr. in 1943 and 24 hr. in 1944 (see Richards and Waloff, 1946), though a small proportion wandered much longer (several weeks). The tendency of wandering larvae to move upwards is well marked, strongly suggesting a negatively geotactic reaction. Wandering larvae will move to the top of an empty glass cylinder, and if this be turned upside down, they will again proceed to the top. If a cylinder is reversed when the larvae are half-way up, most of them turn through an angle of 180° and crawl upwards. This upward drift of larvae is widely quoted in literature (*e.g.* Munro and Thomson 1929; Bovingdon 1933; Reed and Livingstone 1937). Large numbers of larvae can usually be seen on tops of cones and bulkheads, which for a time act as traps. Large concentrations of such larvae are very active—many of them bent upwards at right angles, waving the anterior part of the body from side to side. These movements may be continued for a long time, until in random wandering the

larvae come to the vertical surfaces of walls, pillars or pipes and proceed upwards. This bending of the body upwards is attributed to negative geotaxis—it is rarely seen on the ceiling when the larvae are crawling upside down.

(2) *Negative phototaxis of wandering larvae.* No laboratory experiments on reactions of larvae to light have yet been carried out, but warehouse observations suggest that they are strongly negatively phototactic. Greater numbers of larvae are always seen in the darker parts of the room. The proportions of larvae on sample areas of different light intensities are shown in Table 26. The data in this Table indicate that there is no sharp "discrimination" of the higher range of light intensities, and that the number of larvae increases markedly below 0.009 F.C. However, greater numbers of larvae in dark areas cannot be entirely accounted for by the negative phototaxis of the larvae, but are also affected by the negative light reactions of the ovipositing females.

TABLE 26.
Numbers of larvae in different light intensities.

Description of area	% of total area examined	Dates of weekly samples	Total no. of larvae recorded	Range of light, F.C.	Proportions of numbers of wandering larvae per unit area expressed in % in different intensities of light				
					1 F.C.	0.9-0.1 F.C.	0.09-0.01 F.C.	0.009-0.001 F.C.	0.0009-0.0001 F.C.
1. Wall	4	19.viii.-18.ix.43	2,745	0.8-0.003	—	11.5	23.2	65.3	—
2. Wall	4	24.viii.-10.x.44	14,206	0.122-0.0019	—	13	38.2	48.8	—
3. Ceiling	1.5	19.viii.-18.ix.43	2,425	1.0-0.001	16.2	—	27.5	56.3	—
4. Ceiling	4.5	24.viii.-10.x.44	18,154	0.019-0.0006*	—	—	26.5	40.3	33.2

* Average of two readings.

The negative reaction of larvae to light was expressed in several ways. At the beginning of the wandering stage webbing first appeared on the sides of grain cones away from light; later, as more larvae left the food and wandered, webbing spread to all sides. The following is a list of light intensities taken on the webbed and non-webbed sides of cones.

	On 9.ix.43	Webbed side of grain cone	Non-webbed side of grain cone
Cone 1		0.042 F.C.	0.175 F.C.
" 2		0.07	0.35 F.C. (small amount of web)
" 3		0.065	0.72
" 4		0.12	0.56
" 5		0.003	0.005 (small amount of web)

Again, at the height of the wandering period, steady streams of larvae were seen moving in light gradients on tops of bulkheads, away from the windows. Light intensities of one such gradient were recorded on 10.x.44 at distances 8 ft. apart along the top of a bulkhead.

Negative phototaxis in *E. kühniella* larvae has been described by Brandt (1934), while Klingebiel (1938) has isolated "races" with less ocellar pigment, which do not react to light so readily.

In spite of the well-expressed phototaxis, small aggregations of larvae are

usually seen in uniform diffuse daylight (1.0 + F.C.) near the windows. These larvae when disturbed by touch, move rapidly in directions away from light.

Light intensities.

By the nearest window	Along bulkhead at distances 8 ft. apart						
Light in F.C. 0.61	0.0063	0.005	0.003	0.0013	0.0013	0.0013	Total
No. of larvae on 12.x.44:							
Moving down light gradient	11	7	18	12	16	7	71
Moving up light gradient	3	0	2	0	1	1	7
At right angles to light gradient	1	3	3	0	3	2	12

Positions of larvae in light areas were recorded on three sets of 144-sq. ft. areas nearest to the windows, and as many larvae faced towards light as away:—

	Heads towards light	Away	At right angles
Set 1	48	53	55
" 2	3	8	11
" 3	18	8	9
Total	69	69	75

Further work is needed to explain this anomaly. It must be noted that R. F. Ewer has recorded many more active *E. kühnella* larvae during the day than at night (1943). The kinetic effect of light on *E. elutella* has not yet been studied.

(3) *Hibernation and pupation sites of larvae.* The wandering larvae eventually spin up and diapause in suitable cracks and crevices. The thickness of the cocoons made by the diapausing larvae varies considerably and a small percentage do not spin up at all and remain exposed. In 1943 it was estimated that 97% of the larval population diapaused in the crevices between the ceiling planks. It was usual to find many more larvae in the narrow than in the wide crevices, and laboratory experiments as to the width preference were carried out. The wandering period of 56 hr. (1943) and 24 hr. (1944) appears much longer than would be necessary for a larva to reach a suitable pupation site, but it is probably prolonged by at least three causes: (1) laboratory experiments suggest that the larvae are thigmokinetic and not all crevices are of the width for the tactile stimuli to be satisfied; (2) the arrival of new larvae may disturb some of the larvae already in crevices and hence prolong wandering. This has been observed both in the laboratory experiments and in the warehouse, when larvae marked with dots of paint were released near the occupied crevices; (3) the wandering period may be induced by the physiological state of the larvae, a stage of quiescence not being reached until a certain amount of silk has been lost in wandering.

Laboratory experiments on the choice of crevice width by diapausing larvae.

The crevices were made by placing a required number of small celluloid strips at the ends of two sets of 10 small wooden planks (12.5 × 4.5 cm.). The planks were held tightly together by rubber bands. The width of each crevice was estimated by a screw micrometer and the average of 6 readings

for each crevice was taken. The two sets of planks were placed in circular glass dishes with glass lids. The crevices pointed downwards and the planks were raised 0.5 cm. above the floor by two strips of wood 12.5 cm. long. The glass dishes were kept in darkness at 25° C. 70% R.H. The larvae were released on the floor of each dish and their positions noted 24 hr. later. The results of these experiments are summarised in Table 27.

TABLE 27.

Average width of crevices		No. of larvae in crevices		Same expressed in %	
20 narrow, mm.	20 wide, mm.	Narrow	Wide	Narrow	Wide
1.04	1.53	8	149	5.4	94.6
1.56	2.58	68	56	55.1	44.9
1.59	3.66	110	37	75	25
1.53	4.62	141	17	89.3	10.7

Most of the larvae in these experiments were found in crevices 1.53–1.59 mm. in width. The avoidance of narrower crevices of 1.04 mm. may probably be explained by the fact that this width closely approximates to the depth of the larval head with its setae. The following readings were taken with a screw micrometer :—

	Head capsule		Larval body	
	Width	Depth with setae	Width with setae	Depth with setae
Mm.	0.885	0.972	3.239	2.121
No. of measurements	33	11	10	10

As the body is soft and can be squeezed into crevices, the limit and the preference is provided by the width which allows for head movements in spinning, and yet readily brings the head and setae into contact with solid surfaces.

The positions of 419 larvae in crevices were recorded. Three hundred and thirty-five out of 419 (79.9%) had spun up vertically and 84 (20.1%) horizontally. One hundred and ninety-five (46.5%) of the vertical larvae were in positions with heads up and 140 (33.4%) with heads down. The preponderance of vertically placed larvae and the excess of those with heads upwards is probably the result of negative geotaxis exhibited in wandering. No difference in the date of pupation in the vertical and horizontal larvae has been detected in the laboratory.

Summary of observations on wandering larvae.

1. The fully grown larvae enter a wandering stage which lasts 1–3 days on the average.
2. In wandering the larvae leave a silk trail which they do not appear to follow.
3. The larvae appear to be negatively geotactic, negatively phototactic and thigmokinetic.
4. The choice of a crevice for diapause and pupation is determined by the depth of the head with its setae.

III. DISCUSSION.

The study of the behaviour of this species presented unusual opportunities, as the environment in which the life history is passed is an exceptionally uniform one for a terrestrial animal. Although *E. elutella* feeds on a wide range of foods, the maintenance of the population on bulk grain appears to be due to the chemotactic response of the ovipositing females. In the absence of other foods, these lay on grain in preference to the other surfaces available. The tactile responses at oviposition are only of secondary importance, as in the absence of food the females will lay freely even in completely empty glass tubes.

With this exception of the chemotactic response at oviposition, it was the complex of responses, rather than any single one, that determined the distribution of this species. The behaviour, and the resulting distribution of the feeding larvae in grain, was determined by, at least, the choice of the embryos, and not of the whole grains as food and the interplay of the tactile and positively geotactic reactions. On top of this, crowding induced greater activity which was expressed in the more extensive spreading and the downward drift of the population.

The reactions to light, to temperature gradients and possibly to wind currents, directly affected the distribution of the adults. The reactions to light are complex, for whereas the moths are weakly negatively phototactic, they are immobilised by diffuse daylight, while changes in light intensities, such as occur at sunset and at sunrise, induce great activity and flight, followed by pairing. This periodic activity is thought to be a direct photokinetic response, rather than due to an inner rhythm. It is at these times of flight, and greater activity, that the spreading of the species occurs, and many more moths were seen flying out of the windows at sunset than at other times of the day.

The isolated responses themselves do not remain constant, but change with the physiological state of the insect. Thus, whereas the feeding larvae tend to drift downwards, the fully fed larvae leave the grain and exhibit negative geotaxis. Again, these fully fed larvae rarely spin up in the crevices immediately, but enter a wandering stage lasting 24–56 hours. It is suggested that this wandering period may be induced by a physiological state of the larvae—a stage of quiescence not being reached until a certain amount of silk has been lost in the movement. A clear alteration in the reaction to light is exhibited by the adults, and whereas the young moths aggregate in dark areas, the negative response to light is lost in the older ones, and they drift towards the windows, or to the lighter parts of the experimental box.

Finally, the distribution pattern of the species in a granary can be the combined result of the behaviour of the different stages in the life-history, as the aggregations of the moths in dark areas, and the consequent building up of the populations in these areas, depend not only on the negative phototaxis and restricted activities of the female moths, but also on the negative reaction to directional light of the wandering larvae.

IV. ACKNOWLEDGEMENTS.

Work in the granary was started in 1941–1942 by T. A. Oxley of the Pest Infestation Laboratory, Department of Scientific and Industrial Research, and O. W. Richards. N. Waloff, as a research assistant of Professor H. G. Jackson of Birkbeck College, has been working on *Ephestia* since January 1942, at first with a grant from the Royal Society, but later (1943–1945) under the auspices of the Department of Scientific and Industrial Research.

From the beginning, Professor J. W. Munro has put the facilities of the Department of Zoology of the Imperial College of Science and Technology freely at N. Waloff's disposal, and since 1943 the work has become, in effect, a joint enterprise of the Department of Scientific and Industrial Research and the Imperial College.

The room at the granary and the wheat which it contained were provided by the Ministry of Food through the kind co-operation of Mr. W. McAuley Gracie. Much help in the detailed arrangements was given by Dr. J. A. Freeman, of the Ministry of Food. Our thanks are also due to many members of the Pest Infestation Laboratory staff who have helped in various ways.

V. GENERAL SUMMARY.

1. After the pre-oviposition period of 24 hr. most of the eggs are laid in the first four days of life of the moths. Oviposition takes place in the evening and night in the darker areas of a storage room. The females exhibit marked chemotaxis, and the eggs are laid on grain in the absence of other foods. The ovipositing females are more strongly attracted towards the smell of cacao beans than of grain, irrespective of whether the larvae of the moths were reared on cacao or grain, *i.e.* there appears to be no "habituation."

2. (a) The moths are weakly negatively phototactic, but the reaction is lost as the moths grow older. (b) Moths are inactive in diffuse daylight, but are activated by changes of light intensity at sunset and sunrise. On the whole, it would appear that this periodic activity is not caused by an inner rhythm, but is a photokinetic reaction.

3. The moths are positively thermotactic and react to temperature differences of 3° C. The thermal response overrides negative phototaxis, at least at low light intensities. There are indications that thermo-receptors are located in the antennae.

4. Feeding larvae are mostly found in the upper 30 cm. of grain, but some penetrate to deep layers below 100 cm. Wandering in grain is caused by (a) the need of the larva for about 48 grain embryos, (b) a combination of thigmokinesis and positive geotaxis, (c) mutual activation of larvae in crowded conditions, resulting in more movement, which tends to be downwards.

5. (a) Fully grown larvae enter a wandering stage which lasts 1-3 days on the average. The wandering larvae are negatively phototactic, negatively geotactic and thigmokinetic. They leave silk trails which are not followed by other larvae. (b) The choice of a crevice for diapause and pupation is determined by the depth of the head with its setae.

VI. REFERENCES.

- BARNES, D. F., and KALOOSTIAN, G., 1940, Flight Habits and Seasonal Abundance of Dried Fruit insects. *J. econ. Ent.* **33** : 115-19.
 BOVINGDON, H. H. S., 1933, Report on the Infestation of cured tobacco in London by cacao moth *Ephestia elutella* Hb. *Rep. Emp. Mktg Bd*, No. 67.
 BRANDT, H., 1934, Die Lichtorientierung der Mehlmotte, *Ephestia kühniella*. *Z. vergl. Physiol.* **20** : 646-73.
 CROMBIE, A. C., 1941, On oviposition, olfactory conditioning and host selection in *Rhizopertha dominica* Fab. *J. exp. Biol.* **18** : 62-79.
 DEAL, J., 1941, The temperature preferendum of certain insects. *J. anim. Ecol.* **10** : 323-56.

- DENDY, A., and ELKINGTON, H. D., 1919, On the phenomenon known as "webbing" in stored grain. *Rep. Grain Pests Comm. Roy. Soc.* No. 4, 14-17.
- EWER, R. F., 1943, Diurnal activity of three Insect Pests of stored products. *Nature, Lond.* 152 : 133-4.
- GUNN, D. L., 1940, Daily rhythm and activity of cockroach. *J. exp. Biol.* 17 : 267-77.
- KLINGBEIL, K. H., 1938, Über die Lichtreactionen von Augenmutationrassen den Mehlmotte *Ephestia kühniella* Zell. *Biol. Zbl.* 58 : 631-46.
- MELLANBY, K., 1940, Daily rhythm and activity of cockroach. *J. exp. Biol.* 17 : 278-85.
- MOSSO, M. C., 1932, Pests of stored tobacco in Southern Rhodesia. *Rhod. agric. J.* 29 : 245-65.
- MUNRO, J. W., and THOMSON, W. S., 1929, Report on insect infestation of stored cacao. *Rep. Emp. Mktg Bd.* No. 24.
- NORRIS, M. J., 1932, Contributions towards the study of insect fertility. 1. The structure and operation of the reproductive organs of the genera *Ephestia* and *Plodia*. *Proc. zool. Soc. Lond.* 1932 : 595-611.
- OXLEY, T. A., 1944, The properties of grain in bulk. III. The thermal conductivity of wheat, maize and oats. *J. Soc. chem. Ind. Lond.* 63 : 53-5.
- REED, W. D., and LIVINGSTONE, E. M., 1937, A pest of cured tobacco, *Ephestia elutella* Hb. *Circ. U.S. Dep. Agric.* No. 269.
- REGNIER, R., 1932, Contribution à l'étude de la Pyrale du cacao. *Bull. Soc. Sci. nat. Rouen* 68 : 64-9.
- REH, L., 1907, Insektenfrass an Kakao-Bohnen. *Z. wiss. InsektBiol.* 3 : 21-5.
- RICHARDS, O. W., and WALOFF, N., 1946, The study of a population of *Ephestia elutella* Hübner (Lep., PHYCITIDAE) living on bulk grain. *Trans. R. ent. Soc. Lond.* 97 : 253-98.
- SKALOV, YU. YU., MOROZOV, B. G., ZELENINA, I. N., and PARIEVSKAYA, A. P., 1936, *Pests and diseases of tobacco in Crimea, and their control* (in Russian). Simferopol, Gosizdat, Krim, A.S.S.R.
- STEIN-BELING, I. VON, 1935, Über das Zeitgedächtnis bei Tieren. *Biol. Rev.* 10 : 18-40.
- STRENNIKOV, I. D., 1940, Heat production by movement and its importance in the Ecology of Nocturnal Lepidoptera. (In Russian, English summary.) *Bull. Inst. Sci. Leshaft.* 23 : 293-338.
- THORPE, W. H., 1943, Types of learning in insects and other arthropods. Part I. *J. Psychol.* 23 : 220-34.
- WIGGLESWORTH, V. B., and GILLET, J. D., 1934, The function of the antennae in *Rhodnius prolixus* (Hemiptera) and the mechanism of orientation to the host. *J. exp. Biol.* 11 : 120-39; 408.
- WILLIAMS, C. B., 1939, An analysis of four years captures of insects in a light trap. *Trans. R. ent. Soc. Lond.* 89 : 79-132.

Vol. 97. Part 13. Pp. 337-353, 3 figs.

30th October, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

	PAGE
X BEALL, Geoffrey. Seasonal variation in sex proportion and wing length in the migrant butterfly, <i>Danaus plexippus</i> L. (Lep. DANAIIDAE) . . .	337-353, 3 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 5s.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D. }

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

SEASONAL VARIATION IN SEX PROPORTION AND WING LENGTH IN THE MIGRANT BUTTERFLY, *DANAUS PLEXIPPUS* L. (LEP. DANAIDAE)

By Geoffrey BEALL.¹

Communicated by Dr. C. B. Williams.

Manuscript received 28th June, 1945.

(Read 5th June, 1946.)

WITH THREE TEXT-FIGURES.

In studying the migration of an insect, while it may be difficult, if not impossible, to follow the fortunes of an individual, it may be possible to study populations as wholes. In particular, something may be learned of the occurrence and nature of migration by studying the character of the population, or of successive populations occupying a given territory during successive periods. In the following study the successive populations of the Monarch Butterfly, *Danaus plexippus plexippus* L. occurring in Ontario during the early autumn, in Louisiana later in the season, in California during the winter, and in Ontario again during the high summer, were followed. The two characters, sex proportion and wing length, were considered.

Entomologists seem to have been so impressed by the considerable successes of ornithologists in studying migration by marking individuals that a number of instances are on record of the former marking insects for recovery. While marking probably has its place in estimating the numbers of an insect in a district, or in estimating the rate at which they are leaving a district, from a considerable experience, summarised by Williams *et al.* (1942), its only success so far has been in such studies involving recovery (or non-recovery) in the neighbourhood of the release. The proposed procedure of considering the character of populations may play in the study of insect migration something of the part played in the migration of birds by marking or banding. If precedent counter to that of ornithology is required, it may be found in ichthyology. In some cases tagging has proved very profitable for following fish migration, as in the case of the Pacific salmon, but in others, as for instance the Pacific herring, it was found by Rounsefell (1929) unsatisfactory and he had to fall back on the quantitative study of physical characters to distinguish populations. Butterflies should be more suitable for the studies contemplated than fish, for which growth is continuous, so that considerations of size are complicated by age.

The size of the Monarch Butterfly will, for present purposes, be the length of the right fore-wing from proximal costal angle to most distant point in the apex as discussed and illustrated by Beall and Williams (1945).

In the present work, the character of an entire population will be generally unknown and it will be necessary to rely upon samples for the study. It is important that the samples be as random and unbiased as possible.

Danaus plexippus, with its well-recognised migration, and in the light of recent studies on geographical variation by Beall and Williams (1945), is very suitable

¹ Institute of Paper Chemistry, Appleton, Wisconsin, U.S.A.; formerly of the Dominion of Canada Department of Agriculture, during which service much of the present work was done.

TABLE 1.

The frequency of occurrence of different lengths (in mm.) of the fore-wing of *Danaus plexippus* Linn. from Ontario (Pt. aux Pins) in the autumn.

Mm.	Females										Total	
	31.viii.35	8.ix.35	1.ix.40	7.ix.40	14.ix.40	1.ix.41	8.ix.41	31.viii.43	7.ix.43	15.ix.43		14.ix.43†
43	1	1							1		1	1
44					1		1		1		1	3
45		1		2	1				1	2	2	6
46				4	1					1	4	6
47				8	1				4			20
48		1	3	2	6	2	3	1	10	2	2	26
49		1	5	4	12	4	9	1	16	4	11	54
50	2	7	6	10	14	2	7	9	24	4	24	83
51	11	3	9	8	16	3	11	4	21	10	24	122
52	6	5	7	4	11	2	7	3	15	7	24	107
53	5	5	4	5	9	2	6	2	8	3	8	65
54	5	1	2	2	2	2	5	1	1	1	3	32
55			1	1	1		3				1	10
56												2
57												
n	33	27	38*	50	75	13	54	21	98	34	94	537
Av.	52.4	51.7	51.9	51.8	52.5	51.6	51.9	51.8	51.6	51.8	51.6	51.9
Males												
44												2
45	2	2		1	1		1	1	2		1	1
46	1	1		1	1			1	2		1	5
47									6			6
48									17	2	3	25
49	4	6	2	4	7	5	12	1	14	4	1	48
50	8	1	7	5	9	8	16	5	20	6	8	72
51	8	6	18	10	11	2	9	8	29	8	11	101
52	6	7	9	11	6	4	9	7	13		12	113
53	8	1	8	11	5	1	7	7	7	4	2	75
54	3		4	3	1		5	2	7		2	46
55	3						1	1	5		2	19
56					1		1					2
57			1					1				1
58												1
59												
n	44	27	61	56	45	13	50	36	115	29	49	525
Av.	52.2	51.1	52.9	52.7	52.6	51.9	52.0	52.1	52.1	52.0	52.4	52.3

* On 1.ix.40, one more female was taken but it could not be measured.

† The collection of 14.ix.43 was made at Pt. Pelee, Ontario, some 40 miles uplake from Pt. aux Pins.

material for a study of seasonal variation. Data on sex proportions and size can be related not only to simultaneous observations on its behaviour, but also to a considerable general body of knowledge. Of course, the interest of the present work lies to a considerable extent in technique which might be used on insects suspected of migrating, but on the migration of which direct evidence is elusive, as for example those species that move at night. Thus the economic cottonworm, *Alabama argillacea* Hübner, is believed to leave Peru and to reappear in the United States, but means of following its movements are required. Again, lines of work that prove useful for *D. plexippus* might be followed in the case of a sphingid, *Phlegethontius quinquemaculata* Haworth, the Tobacco Worm, which breeds as far north as Canada, and which is also suspected of migration.

Here and there in the following discussion it will be noted that the author is indebted to Dr. C. B. Williams for assistance, but it should be explained that the entire study was carried out with Dr. Williams' advice and encouragement so that the debt is far more considerable than might be realised without the present statement.

2. THE MIGRATING AUTUMNAL POPULATION IN ONTARIO.

Consider first the character of the young autumnal migrant Monarchs that pass through Ontario in early September. Extensive and systematic collections are available from Pt. aux Pins on the northern shore of Lake Erie, the situation and conditions of collecting being described by Beall (1941a). The primary data on wing length and number captured are shown in Table 1, for which the totals have previously been published by Beall and Williams (1945). Below each panel there is shown n , the number of butterflies involved and also $\bar{A}v$, the average length of the wings in mm. The date shown against each collection is that of the evening of the formation of the clusters of the migrant Monarchs on trees from which collections were made once a week. These collections were probably a fair sample, particularly of the sex proportions, since they were made at sunset or sunrise when the butterflies in the clusters were quiescent. Further data from Ontario, on the summer breeding population, will be treated in Sect. 5, because it seems, from the trend of flight established by Beall (1941b) for Ontario, that they probably deal with a population immigrant from the South.

Among the migrating Monarchs in the autumn, the proportion of the total catch (Table 1) at Pt. aux Pins that was female came, each year, to form an increasingly large part of the population as the season advanced. The percentage female from each collection is summarised in Table 2. The time intervals of Table 2 are of a week, and it will be seen that every week in 8 cases the proportion of females rose; the differences average 8%. Statistically ²

² An adequate, although not powerful, test of the significance of the effect observed is provided by treating the results for each year as a problem of contingency and then considering the joint probability for all years. Thus consider the two collections for 1935:—

Date	Females	Males
31.viii. . . .	33	27
8.ix. . . .	44	27

This contingency table can be tested for homogeneity by the χ^2 test; thus we find (using in this case of only 2 observations, the modified theory of Yates 1934) that with one degree of freedom $\chi^2 = 0.396$ and that the probability, P_{χ^2} , of so great a value of χ^2 having arisen

there was a significant change in sex proportions. The tendency for females to form a large part of the population by the middle of September is shown, further, by the supplementary collection (shown to the right of Table 1) on 14th September, 1943, at Pt. Pelee, Ontario, where 62% of the population was female. A tendency for the sex proportions of migrant butterflies to change with time is indicated by the records summarised by Williams (1930: 346),

TABLE 2.

The percentage female at Pt. aux Pins, by date.

1935	31.viii. 43%	8.ix. 50%	
1940	1.ix. 39%	7.ix. 47%	14.ix. 63%
1941	1.ix. 50%	8.ix. 52%	
1943	31.viii. 37%	7.ix. 46%	15.ix. 54%

but the matter does not seem to have been followed closely in the field. Whether the change, in the case of the Monarchs, was due to a tendency for the females and males to migrate at different rates, or whether it was simply due to the replacement of one population by another with different sex proportions, we cannot say; certainly the immature forms were so rare locally, as discussed by Beall (1941a), that we cannot believe it due simply to a difference in a local rate of emergence of pupal females and males.

It is, of course, most important that a uniform method of collecting be employed, otherwise large differences in sex proportion may arise artificially. In the present work, the collections were made consistently from quiescent clusters so that it may reasonably be supposed that the sexes stood the same chance of being taken. In some insects the relative length of life of the two sexes might introduce a changing ratio as migration progressed but, again, no such objection can be raised in the case of Monarchs that live until the following spring.

Having considered the change in sex proportions, let us now consider change in the size of butterflies, during the southward migration. From the average

by chance is 0.53. A similar calculation can be made for each year with the result as follows:—

	1935	1940	1941	1943
χ^2	0.396	12.668	0.002	3.762
Probability	0.53	0.0015	>0.9	0.12

From these results, although it can be seen that in no single year except 1940 was the change in sex proportion so marked that it could confidently be considered significant, the joint effect over all years was so, i.e., the sum of the 4 values of χ^2 is 16.83 with a significant probability of 0.01. Hence considering the results for all 4 years, a real variation in sex proportion occurred. If a more powerful test, making allowance for the common direction of the change, had been employed, the result would have been more highly significant.

length of wing, for each sex in Table 1 for each collection, it appears that, in spite of the foregoing evidence from sex proportions of migration during the

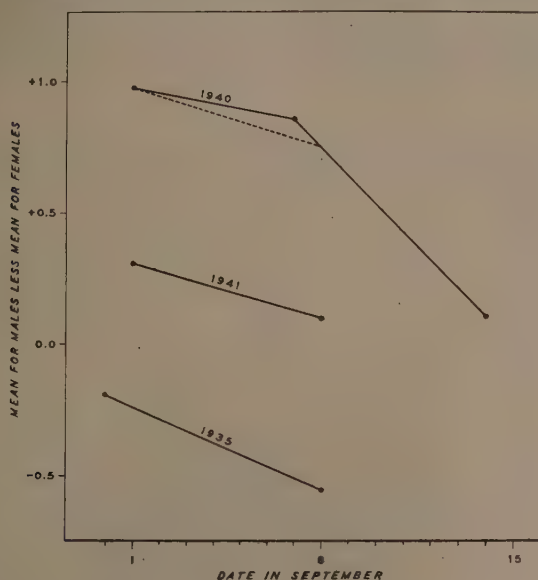


FIG. 1.—The difference in average wing length for males and females at Pt. aux Pins.

period of observation, the mean wing length was fairly steady from one collection to another. Statistical³ analysis shows there to have been no significant change either within the seasons or between the seasons or years. The uniform-

³ The analysis, appropriate to the present case, of variance within collections, between collections, and between years, for variable numbers of observations within collections, follows the line indicated by Beall and Williams (1945). The result is as follows:—

Variability	Females		Males	
	<i>f</i>	Mean sq.	<i>f</i>	Mean sq.
Within collections .	433	4.16	466	4.45
Between collections .	6	4.18	6	3.67
Between years .	3	6.21	3	19.50

where the mean square within collections (for females and males respectively) is simply the estimate of squared standard deviation for a single day and the mean squares between collections and between years are comparable quantities. It can be seen that the variability between collections is not significantly greater than that within collections, so that there is no significant evidence that the wing length was changing between collections within a year, and apparently during the autumn there occurred successive populations, all having essentially the same wing length. Between years the variability is great for males and if the variance ratio, $F = 19.50/4.45 = 4.38$ is referred (for $f_1 = 3$, $f_2 = 466$) to a table such as that of Snedecor (1934), it is found to lie a little beyond the 0.01 level of probability. When the result between years for females is considered jointly, however, with males, even this variability between years is not significant.

ity of the material gathered in 4 seasons over 9 years should be borne particularly in mind. Such uniformity of material, from year to year, is the more remarkable because, as has been shown by Beall and Williams (1945), Monarchs collected in various parts of North America varied very appreciably. The autumnal material collected at Pt. aux Pins apparently originated under conditions so stable that a very uniform type of butterfly resulted.

TABLE 3.

The difference (males minus females) in average wing length, in mm., at Pt. aux Pins.

1935	31.viii. -0.197	8.ix. -0.556	
1940	1.ix. +0.974	7.ix. +0.856	14.ix. +0.098
1941	1.ix. +0.308	8.ix. +0.096	
1943	31.viii. +0.274	7.ix. +0.472	15.ix. +0.270

Although there was found no significant variation of wing length within a single autumn, a curious effect is suggested by the present data, *i.e.*, the difference in the mean length of the wing for the two sexes appears to change systematically. In the first place, it is obvious from Table 1, that males were very slightly the larger. From the data of Table 1, during the week or two of observations each year, apparently the males tended to be the bigger at the beginning of the flight and the smaller at the end (just as the proportion of males fell). The situation may be appreciated by considering the differences of average wing length of males less that of females, as in Table 3. The result is illustrated in fig. 1. An indication of this effect is merely advanced as a suggestion to be borne in mind as worthy of consideration when material similar to the present, *i.e.*, showing in particular a change in sex proportions, is collected elsewhere.

3. MIGRANTS OF THE AUTUMN IN LOUISIANA.

After the great flights of Monarchs that occur in Ontario during September, there are later flights, presumably of some northern material, about a month later far to the south. We are fortunate in possessing two very satisfactory collections made in Louisiana, from clusters at a single time on each occasion, one on 29th Oct. 1938 and the other on 7th Nov. 1941, and sent with the greatest kindness by Mr. Percy Viosca of the Southern Biological Supply Co., of New Orleans. Almost all the collections were made from great aggregations at North Shore, on the north side of the east end of Lake Ponchartrain, but a few were made in the earlier year at nearby Gentilly on the south side of the lake. In Table 4, the wing measurements of this Louisiana material are shown.

In Table 4, it can be seen that the proportion of females, 33%, is below that of any collection shown in Table 2 from Ontario. There was further no significant differences in the proportions for the two years ($\chi^2 = 0.90$). Whether the low proportion signifies that the flights in Louisiana corresponded to a very early phase of the migration in Ontario, whether the males tend progressively to outfly the females in the long journey to the south, or whether more females than males are lost cannot be said.

From the average values of Table 4 it is plain ⁴ that although the two flights in Louisiana were separated by 3 years, they yet consisted of surprisingly similar material. The smaller butterflies of Table 4 were as typical of Louisiana as were those of Table 1 for Ontario.

It is also plain from Table 4 that the Monarchs of Louisiana were smaller than those from Ontario. So we cannot reasonably suppose that the Monarchs

TABLE 4.

The frequency of occurrence of different wing lengths of *Danaus plexippus* Linn. from Louisiana (North Shore) late in the autumn.

Mm.	Females			Males		
	29.x.38	7.xi.41	Total	29.x.38	7.xi.41	Total
44		1	1			
45				3	1	4
46				2	1	3
47	1		1		2	2
48	1	2	3		2	2
49	1	3	4	2	1	3
50	6	2	8	9	4	13
51	6	3	9	12	6	18
52		7	7	5	8	13
53		1	1	4	5	9
54				2	1	3
55						
56					1	1
<i>n</i>	15	19	34	39	32	71
<i>Av.</i>	50.0	50.4	50.2	50.4	50.8	50.6

Two more specimens of each sex were taken on 17.xi.41, but they could not be measured.

of Table 1, that left southern Ontario in early September of 1941, were the same as those that appeared in Louisiana in early November of the same year. Further, it should be noted that the material from Louisiana was no more variable ⁵ than that from Ontario; indeed, the two lots are practically equally variable. Since the Louisiana population was as homogeneous as that of Ontario, it is clear that it did not have a smaller average wing length than the Ontarian because of the admixture of a population having small wings with material like that of Ontario. We may not therefore suppose that it consisted of any appreciable amount of Ontarian material plus recruits from smaller populations gathered on the way.

⁴ The analysis of variance for the Louisiana data is:—

Variability	Females		Males	
	<i>f</i>	Mean sq.	<i>f</i>	Mean sq.
Within collections	32	3.26	69	5.53
Between collections	1	1.14	1	2.92

from which clearly there was a very high resemblance between the two collections.

⁵ The mean squares from the preceding analysis of variance within collections are for females 4.16 and 3.26 in Ontario and Louisiana, respectively, and for males, 4.45 and 5.53.

4. THE WINTER RESIDENT POPULATION IN CALIFORNIA.

Great flights of Monarch Butterflies originate in the north and, presumably, come to rest in Florida and California. Of one winter resident population, that of California in the seasons 1937-38, 1938-39 and 1941-42, we have samples.

TABLE 5.

The frequency of occurrence of different lengths of the right fore-wing of *Danaus plexippus* Linn. from California, collected in various months as indicated.

Females											
Mm.	x.37	xii.37	ii.38	iii.38	iv.38	v.38	x.38	i.39	ii.39	ii.42	Total
40				1							1
41											
42							1				1
43											
44		1	1								2
45		1									1
46	1	1		1							3
47	1	1									2
48	2	1			1		1			3	8
49	1	8	3				2			3	17
50		2	2	2			1	1	1	4	13
51	1	1	3			1	3	1	2	5	17
52		2	2		1		1	1	2	3	12
53	1	1	2	2				3	1	3	13
54			1	1			1	1	1		5
55		1	1						1		3
n	7	20	15	7	2	1	10	7	8	21	98
Av.	48.9	49.2	50.9	49.4	—	—	49.7	52.3	52.2	50.5	50.3
Males											
43		1	1								2
44		1								1	2
45	3	2							1		6
46	2	1		1						3	7
47	4	2	1		1					1	9
48	3			3			1			10	18
49	2	3	1	2		2			1	11	22
50	1	5	1	4	1	1	2	1	1	14	31
51	2	2		1	2	2	3	1		17	30
52	2	1	1	4	1		2	1	3	19	34
53		4		1			2	3	4	6	20
54		2	3					1		4	10
55	1			1		2				1	5
56				1							1
57		1									1
n	20	25	8	18	5	7	10	7	11	87	198
Av.	48.4	49.8	50.4	50.6	50.2	51.4	51.1	52.3	50.9	50.5	50.3

So far as California is concerned, we shall refer to a season as the period starting in October with the arrival of migrants and running over the winter resting period to May of the following year, when the Monarch becomes rare. The material most strictly comparable with that of Ontario was furnished by Pro-

fessor Harry S. Smith, of the Citrus Experiment Station at Riverside, California, who, with the greatest kindness, sent a collection of 108 Monarch Butterflies taken at Ventura, which is well south in California. The butterflies had been collected by Dr. Paul de Bach and Dr. D. C. Lloyd on 24 Feb., 1942, at night, and very early next day before the insects could fly, by knocking them from tall cypress trees with sticks. In Table 5 the wing measurements of this and other material are shown according to the year when they were caught. The other Californian material measured by Dr. C. B. Williams and most generously given the author, was collected by Mr. J. A. Downes (in large part) and by Messrs. A. Forbes and M. Duperu at Pacific Grove (in large part), Bolinas, El Cerrito, San Francisco, San José, Owen Valley and San Diego.

The subject of sex proportions of the Monarch Butterfly in California during the winter has been discussed at some length by J. A. Downes, in Williams *et al.* (1942: 165), who found the females at Pacific Grove to constitute about one-third of the population during the winter and less during and after March. From Table 5 it will be seen that in 1942 the proportion of females (19%) was even lower than in Downes' experience. The low proportion of females among Monarchs that winter in California is surprising if we suppose they originate in some region like Ontario, where the proportion of the two sexes is about equal, as shown in Table 2 (males predominating at first but females later). It should be borne in mind, however, that the systematic collections made in Ontario of migrants at Pt. aux Pins were restricted to the great flights of September. No counts were made of a thinner flight which occurs during October and even occasionally into November; the occurrence of this flight has been noted at the Southey Shoals Lighthouse off Pt. Pelee. Accordingly, some caution must be exercised in generalisation about the trend of sex proportions for Ontario during the unexplored later season of flight. In so far, however, as the females do migrate later in the season than the males, we may suppose that their losses will be greater (the passage presumably becomes increasingly hazardous) and so we may perhaps account for an excess of males at the journey's end.

One further collection, for which the measurements are shown by Beall and Williams (1945), from Sedan, Minnesota, in September, was made from great dormant clusters like those of Ontario, and presumably furnished a good sample of the sex proportions; females comprised only a third of the catch. This proportion is similar to that in Ontario at the beginning of the autumnal flight and also in Louisiana at the beginning of November. This deficiency of females in Minnesota and Louisiana may merely represent a phase of the migration, or on the other hand may be related to some permanent deficiency like that of California, where no question of such phase arises.

It might be feared that a comparison, with regard to wing length, of the Californian material, examined in large part by one worker, Dr. C. B. Williams, with Ontarian material examined by the author would be invalid on account of personal differences. Such a comparison of all Californian material with all Ontarian will not be made, but it should be pointed out that since the data of the third season (1942) in California (measured by the author) are intermediate between the means for the first two seasons (measured by Dr. Williams), the procedure of the two workers was probably substantially the same.

Considering the average length of wings for each sex, in Table 5, we see signs of heterogeneity within a season, which proves statistically⁶ to be sig-

⁶ The homogeneity of material, within seasons by months, may be found for the

nificant. This results means that the population changes its character during the period of winter rest. It is difficult to guess why such a change should occur. The question was referred to Mr. J. A. Downes of the University of Glasgow, who has studied the Monarch in California (Williams *et al.* 1942) and he has assured the author, by private communication, first, that certainly there is no local emergence during the winter at Pacific Grove, and even at Los Angeles or San Diego it is only possible that 1 in 1000 (no more) winter-caught butterflies have emerged recently. Mr. Downes considers, secondly, that there is little possibility that any slight movement up to the end of March could account for any change in the nature of the population. The only probable explanation to present itself is that there was some differential death rate for butterflies of various wing-spread. Such a supposition has support from data (shown in an appendix to the present work) on the wing spread of Monarch Butterflies lost in the flight over Lake Erie. Those lost tend to be the butterflies with shorter wings.

For California, the variability ⁷ (mean square) within months was not constant from year to year. The variability within months was significantly the bigger in the first season. The difference in variability can perhaps be appreciated from the data of Table 5, but to point the matter, the total collections for the two seasons by sexes have been plotted in fig. 2. Any variability introduced in the figure by differences between months is trivial.

The great variability in the first season of 1937-38 deserves some consideration, for such variability is just that which would arise if populations of different average size were mixed. We might suppose that the population of the first season was so variable because it consisted of two superimposed populations differing by about 4 mm.⁸ in their average value. Accordingly, if one of the

Californian material as for the Ontarian material with the reservation that the analysis be made separately for each year. The analysis of variance is as follows:—

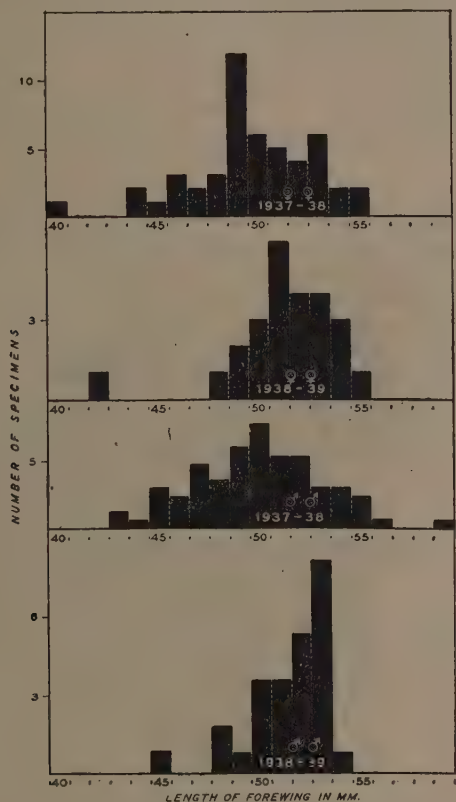
Variability	1937-38				1938-39				1941-42			
	Female		Male		Female		Male		Female		Male	
	<i>f</i>	M. sq.	<i>f</i>	M. sq.	<i>f</i>	M. sq.	<i>f</i>	M. sq.	<i>f</i>	M. sq.	<i>f</i>	M. sq.
Within months .	45	9.11	77	9.64	22	5.59	25	4.05	20	2.66	86	4.18
Between months .	3	9.98	5	14.54	2	19.77	2	4.43	—	—	—	—

In only one case, females of 1938-39, is the mean square between months significantly greater than within months, but it is somewhat the greater in all 4 cases (of 2 sexes in each of 2 seasons), so that the joint effect is significant.

⁷ Consider particularly the variability, within months, for the first two seasons (1937-38 and 1938-39) of which the conditions of collection and examination are most closely the same, as has been previously indicated. Comparing the appropriate mean squares in the preceding analysis of variance, we find, for the females, $F = 9.11/5.59 = 1.63$ ($f_1 = 45$, $f_2 = 22$), which is big but not significant. For the males in a similar way, between the first two years we find $F = 2.38$ ($f_1 = 77$, $f_2 = 25$) which is a little beyond the 0.01 level of significance and hence clearly significant.

⁸ The value of 4 mm. depends on two assumptions, which, while unproven, are convenient, reasonable and instructive. First, we assume the two constituent populations equally represented. Secondly, we assume the variability of each population to be represented by a standard deviation of 2 mm. In the latter connection, the second and third seasons did have such a standard deviation as did the collections from Ontario.

populations in California of 1937-38 were as large as the Monarchs of Ontario (the largest we have seen), *i.e.*, about 52 mm., the other would be 48 mm., which is as small as those from the Canaries, of Beall and Williams (1945), one of the smallest on record. Indeed the average of the composite population would only be about 2 mm. less than that of the larger constituent population



2

FIG. 2.—The total distributions of wing length of Monarchs for the seasons 1937-38 and 1938-39 in California.

and that difference is of the same magnitude as the observed difference between the two seasons, 1937-38 and 1938-39.

It will be noted from the comparison of the average values of Tables 1 and 5, that the wings of the Californian material, while somewhat variable, appeared rather shorter than those of the Ontarian material. For one Californian collection, that of the winter of 1942, the catch is strictly comparable with that (from two collections) of Ontario in the preceding autumn, in that the same butterflies might have been involved. Statistically the difference is highly significant for each sex separately and, of course, for the two jointly. Thus we

see clearly that the butterflies taken at Pt. aux Pins, Ontario, in the autumn did not belong to the same population as that in Ventura, California, during the following winter. No other data were collected in the two places which were so strictly comparable.

From Table 5 it appears that the Monarch Butterflies in California differed considerably from year to year as proves statistically⁹ to be the case. The butterflies of the first season were the smallest. For 1942, the means lay between those of the other two seasons, as can be seen from Table 5. The probable heterogeneity of the Californian population is somewhat surprising in view of the homogeneity of the autumn population in Ontario, as is discussed in Sect. 2. Such changes in wing length from one year to another suggest that the winter residents of California may originate in various regions.

5. THE SUMMER BREEDING POPULATION IN ONTARIO.

We unfortunately possess no extensive material taken from the flights to the north in the early spring and so must complete the cycle of the Monarch's year with collections made in high summer from the breeding population in Ontario. The material to be considered was collected near Chatham, on 11, 12, 13 + 14, 15, 16, 20 and 21 July, 1941, at which time (Beall, 1941a) the population is sexually mature and probably engaged (Beall, 1941b) in a north-westerly migration. This collection was made at the earliest date at which it was found possible to obtain Monarchs in any numbers, but it was some 6 or 8 weeks after the first Monarchs appear in the district. Accordingly, these collections unfortunately do not bear unquestionably on the long moot point of whether the Monarchs that appear in the spring are of the group that leaves the north in the autumn, since it is possible that these butterflies were not the first generation in Ontario. From the relatively good condition of the butterflies, of which many males in particular were quite fresh, it was hard to believe that they had indeed gone south 10 or 11 months before. On the other hand, there was no possibility of confusing them with the radiant and perfect specimens involved in the migration a month or so later. These collections were necessarily made by taking the Monarchs on the wing, rather than by taking quiescent aggregations, as in the autumn. The wing length for these catches was as shown in Table 6.

The data of Table 6, on the summer material in Ontario, give no indication¹⁰ of heterogeneity in the sex proportions and hence no indication of migration, which was probably not to be expected. The test in the present case, however, bears upon the necessarily suspect procedure of sampling by taking insects on

⁹ The comparison of the average values of wing length between years is complicated by the circumstance, just discussed, that the variability within years differs so much. The situation may, however, be considered roughly as follows:—

	Females	Males
1937-38 mean, $\bar{x}_1$	49.7	49.9
1938-39 mean, $\bar{x}_2$	51.2	51.3
Diff. between means, $d = \bar{x}_2 - \bar{x}_1$	1.5	1.4
St. error of diff.	0.68	0.52
$d/s.e.$	2.3	2.8

In view of the very considerable number of observations involved, the final values 2.3 and 2.8 may be regarded as normal deviates with unit standard deviation and so definitely significant.

¹⁰ Setting up a contingency table of sex against time, from Table 6, $\chi^2 = 4.91$ ($f = 6$) and $P_{\chi^2} = 0.56$, so there is clearly no heterogeneity.

the wing. The result is reassuring, for since on 8 days the sexes were taken in quite an unbiased way, then surely the various types of a given sex must have been taken fairly. Such was probably the case, for a limited area (about a

TABLE 6.

Frequency of occurrence of different lengths of the fore-wing of *Danaus plexippus* Linn. collected during July, 1941, near Chatham, Ontario.

Females								
Length in mm.	11	12	13 & 14	15	16	20	21	Total
46			2	1				3
47			1	1	2			4
48			2	1	1	1		5
49		1	1	3				5
50	1	2	2	2	1	2	3	13
51	2		2	2	3	6	4	19
52	1		8	4	1	8	4	26
53			2	3		3	5	13
54	1		3	2	1	4		11
55	1	2	1	1				5
<i>n</i>	6	5	24	20	9	24	16	104
<i>Av.</i>	52.2	51.8	51.0	51.0	50.1	51.9	51.7	51.3
Males								
46						1		1
47			1					1
48	1	1	1				1	4
49			2			2	1	5
50		1	3	1	1	3		9
51	2	4	7	6	11	11	7	38
52		2	4	6	3	7	8	30
53	2	4	12	4	2	16	5	45
54		1	6	3	3	9	3	25
55		2	1	4	1	4	3	15
56	1		1	1		1	1	5
57				1				1
<i>n</i>	6	15	38	26	11	54	29	179
<i>Av.</i>	52.0	52.1	52.1	52.9	52.7	52.4	52.3	52.4

quarter of a mile along a drainage cut) was patrolled all day, and practically all the Monarchs present there each day were taken.

The catch for the summer was further quite homogeneous¹¹ with respect to wing size.

¹¹ The appropriate analysis of variance is:—

Variability	Females		Males	
	<i>f</i>	Mn. sq.	<i>f</i>	Mn. sq.
Within days . .	97	4.43	172	3.43
Between days . .	6	5.40	6	2.20

Turning now to the comparison of the two seasons, the summer of 1941 and the preceding autumn of 1940, as from Table 1, we find the following average values for wing length:—

Females		Males	
1940 autumn	1941 summer	1940 autumn	1941 summer
52.1	51.3	52.7	52.4

where the joint result is probably significant,¹² although slight. The variability of the summer material was, if anything, smaller than that of the autumn material, which suggests that a very homogeneous population reared in one place was present. These results indicate that the population of Monarchs which appeared in the summer was not the same north-bred population that disappeared in the preceding autumn, but rather some population bred, subsequently, probably in a fairly limited region to the south. Fig. 3, where the two populations under consideration at the moment are plotted, illustrates the small but perceptible shift in wing length.

6. DISCUSSION.

It may be profitable to emphasise two directions in which the present work on the Monarch Butterfly could best be extended, and two other points where the results obtained so far may be of use in dealing with other insects.

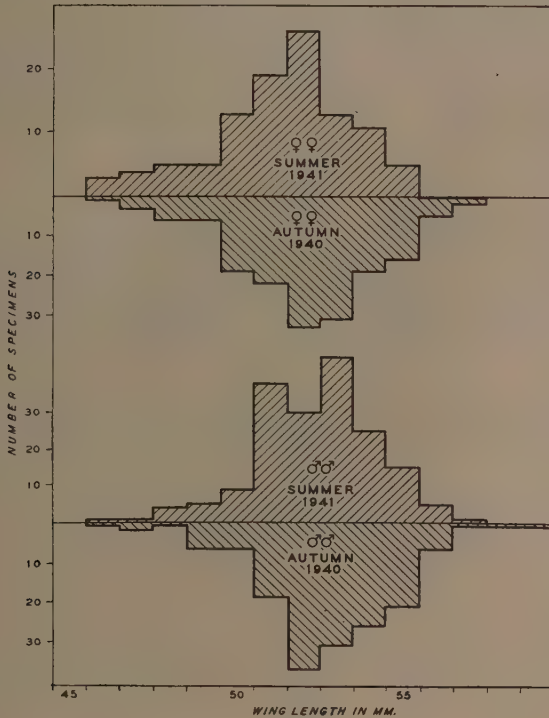
One of the principal conclusions to be drawn from the collections, particularly those made in Ontario, is that there came regularly during a season and from year to year a very uniform type of butterfly, as judged by wing length, characteristic of the region. Equally extensive parallel collections of the Monarch elsewhere, say from Minnesota or New England, would be desirable to discover whether other regional populations are equally stable. It would then be possible to speculate on the origin of flights occurring in, say, New Orleans. The possibility of certain interchanges of population could be dismissed while others would be judged more probable. It has been pointed out that the peculiar sex proportions of the Monarch Butterfly in their wintering place, California, possibly arise in the southerly flight, *i.e.*, there is a marked difference in the proportions for Ontario and Louisiana. Accordingly, it would be very desirable if the matter of sex proportions could be investigated further by successive observations during a season at places far to the south and from collections intermediate between such places as Ontario and Louisiana.

¹² Making an analysis of variance, as previously:—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Within seasons . . .	265	4.52		339	3.76	
Between seasons . . .	1	40.74	9.01	1	10.66	2.83

where jointly the values of *F* have a probability of 0.002.

The present work has brought out in two places statistical evidence of migration that might be paralleled by insects undertaking a hidden migration, such as the Tobacco Worm, *Phlegethontius quinquemaculata* Haworth, possibly makes at night. This species was mentioned in the introduction as one of which the migration might be studied statistically. A change of wing length or of sex proportions might be accepted as evidence of migration, with a degree of assurance depending on the character of the change. Thus we have the illustration in Ontario, between summer and autumn, of a change in average size without an increase or decrease in heterogeneity and hence clear evidence



3

FIG. 3.—The distribution of wing length for the collections in the autumn of 1940 and the summer of 1941, in Ontario.

of a replacement of populations. Again, the present results from California, where the material shows distinct signs in one year of consisting of a mixture of two very different populations, are encouraging in suggesting that it may be possible to identify a region as the terminal point of a migration. Thus in the case of *Phlegethontius quinquemaculata* it might be anticipated that the superimposition of southern migrants on a north-bred population would result in abnormal variability in the population.

7. REFERENCES.

- BEALL, G., 1941a, The Monarch Butterfly, *Danaus archippus* Fab. I. General observations in southern Ontario. *Canad. Field Nat.* 55 : 123-9.
- 1941b, The Monarch Butterfly, *Danaus archippus* Fab. II. The movement in southern Ontario. *Canad. Field Nat.* 55 : 133-7.
- and WILLIAMS C. B., 1945, Geographical variation in the wing length of *Danaus plexippus*. *Proc. R. ent. Soc. Lond.* (A) 20 : 65-76.
- ROUNSEFELL, G. A., 1929, Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska. *Bull. U.S. Bur. Fish.* 45 : 227-320.
- SNEDECOR, G. W., 1934, *Calculation and interpretation of analysis of variance and covariance*. Collegiate Press, Ames, Iowa, 96 pp.
- WILLIAMS, C. B., 1930, *The migration of butterflies*. London, xi + 473 pp.
- , COCKBILL, G. F., GIBBS, M. E., and DOWNES, J. A., 1942, Studies in the migration of Lepidoptera. *Trans. R. ent. Soc. Lond.* 92 : 101-283.
- YATES, F., 1934, Contingency tables involving small numbers and the χ^2 test. *J. R. statist. Soc. Suppl.* 1 : 217-35.

APPENDIX.

THE CHARACTER OF MONARCHS LOST IN THE CROSSING OF LAKE ERIE.

The present work has been concerned with the character of populations of Monarch Butterflies to be found in various places and at various times, but it seems reasonable to add the present appendix on the character of the butterflies

TABLE 7.

Frequency of occurrence of different length of the fore-wing of *Danaus p. plexippus* L. cast upon Pt. aux Pins, from Lake Erie on 13.ix.1943.

Length in mm.	Females	Males
39		1
—		
46	1	
47		2
48	1	1
49		3
50	1	2
51	3	4
52	1	5
53	3	3
54	1	1
<i>n</i>	11	22
<i>Av.</i>	51.1	50.2

lost in the crossing of Lake Erie. From time to time considerable numbers of insects are cast up on the shore of Lake Erie, and from such material found in the afternoon of 13 September 1943 at Pt. aux Pins, the Monarchs were selected for study. It may be noted that 57 more or less entire butterflies were found dead just above the water-line in a walk of $1\frac{1}{2}$ miles along the beach. The sex of two of these could not be determined; of the 21 females found, in only 11 could the wing length be measured, and of the 34 males, in only 22 could the length be measured; the data on wing length are shown in Table 7.

It may be remarked that the low fraction of females found, 38%, is in reasonable accordance with the fraction, 46%, taken from clusters formed on 7 September, 1943, or with 54%, taken from clusters found on 15 September, so that there is no clear evidence of differential death rates with sex.

It is noteworthy that for both sexes the average wing length in Table 7 was lower than in any other collections ever made in Ontario in the autumn. It is apparent statistically ¹³ that the difference in size between the present lot thrown up and those of the preceding collection from clusters of 7 September, 1943 (as in Table 1), is significant, *i.e.*, that the Monarchs thrown up on the beach were smaller than those of the general population. A powerful selective effect may operate in flight across Lake Erie. Records on the selective effect of migration are of such general importance that the present matter would be worthy of further investigation when butterflies are again thrown up.

¹³ The analysis of variance is:—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Within lots . . .	107	3.77	1.30	135	4.83	
Between lots . . .	1	2.90		1	65.07	13.46

when the probability of *F* is about 0.6 for females and 0.001 for males; jointly the effect is significant.

Eu. 344.

Vol. 97. Part 14. Pp. 355-379, 21 figs.

15th November, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

- X ASHBY, D. G., M.A., and WRIGHT, D. W., M.A. The
immature stages of the carrot fly . . . 355-379, 21 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.
C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.
H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.	CAPT. R. A. JACKSON, R.N.
J. W. EVANS, M.A., D.Sc.	MISS C. E. LONGFIELD.
G. FOX-WILSON, N.D.H.	SIR GUY A. K. MARSHALL, K.C.M.G.,
R. M. GREENSLADE.	D.Sc., F.R.S.
FRANCIS HEMMING, C.M.G., C.B.E.	G. E. J. NIXON, B.A.
H. E. HINTON, B.Sc., Ph.D.	J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.	W. RAIT-SMITH.
FRANCIS HEMMING, C.M.G., C.B.E.	O. W. RICHARDS, M.A., D.Sc.
H. E. HINTON, B.Sc., Ph.D.	

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.	J. SMART, B.Sc., Ph.D.
B. M. HOBBY, M.A., D.Phil.	W. H. THORPE, M.A., Sc.D.
J. F. PERKINS, B.Sc.	

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.	O. W. RICHARDS, M.A., D.Sc.
K. G. BLAIR, D.Sc.	N. D. RILEY (<i>Secretary</i>).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.	A. M. MASSEE, D.Sc.
E. A. COCKAYNE, M.A., M.D., F.R.C.P.	THE HON. MIRIAM ROTHSCHILD.
CAPT. R. A. JACKSON, R.N.	W. H. THORPE, M.A., Sc.D.
COL. F. A. LABOUCHERE.	N. D. RILEY (<i>Secretary</i>).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

- 1. British National Committee for Biology** (Royal Society).
Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.
Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.
- 2. Local Committee of Management of Wicken Fen.**
Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].
- 3. National Trust for Places of Historic Interest or Natural Beauty.**
Mr. H. M. Edelsten, O.B.E., appointed 1944.
- 4. New Forest Association.**
Mr. W. Fassnidge, appointed 1934.
- 5. New Forest Joint Committee.**
Mr. W. Fassnidge, appointed 1939. *Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.*
- 6. Royal Meteorological Society. Phenological Committee.**
Dr. C. B. Williams, M.A., D.Sc., appointed 1937.
- 7. Biology War Committee.**
Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.
- 8. Council for the Promotion of Field Studies.**
Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.
- 9. Joint Bioclimatic Committee.**
Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

THE IMMATURE STAGES OF THE CARROT FLY

By D. G. ASHEY, M.A.

(School of Agriculture, Cambridge),

and

D. W. WRIGHT, M.A.

(Horticultural Research Station, Cambridge, and School of Agriculture, Cambridge).

Manuscript received 2nd April, 1946.

(Read 5th June, 1946.)

WITH 21 TEXT-FIGURES.

DURING the course of an investigation on the biology and control of the carrot fly, the opportunity occurred to obtain a more complete knowledge of the various immature stages of this insect. Accordingly, material and data were collected from the main carrot-growing areas of East Anglia during 1942, 1943 and 1944. Most of the work has been done on alcohol-preserved material, and for that reason the internal anatomy of the larva has not been studied; the histological and embryological aspects have also been omitted.

The drawings have been made with the use of a gridded micrometer eyepiece, and the scale (in most cases 0.1 mm.) is appended to each figure.

The carrot fly studied has been *Psila rosae* Fabricius. The larva is generally found attacking the root of the carrot, though other hosts, both wild and cultivated, are known to occur. The biology of the insect is described in a recent paper by Petherbridge and Wright (1943).

THE LIFE HISTORY.

As a background to the description of the various stages a brief account will be given of the life history. The eggs are laid, singly or in small groups, usually not more than half an inch below the soil surface and within an inch or two of the host plant. The eggs hatch to liberate the first-instar larva, the form of which is clearly discernible in a prepared specimen through the chorion of the egg. The larva begins to feed shortly after eclosion, and enters the tap or side roots of the host. Evidence suggests that moulting occurs only when the larva is free in the soil (migrating), and not while it is in the host, for cast skins were not found in a damaged host root, though they would be made visible by the presence of the dark hind spiracles on the cast skin.

On becoming fully fed, the larva leaves the host and enters upon the quiescent puparial stage in the soil. Inside the puparium, which is found in the upper 6 inches of the soil (Petherbridge & Wright, 1943), the de- and re-differentiation of larval tissue and the further development of the imaginal buds take place to form first the true pupa and later the imago. The imago, when ready to emerge, ruptures the puparial case along the line defined at the time of puparium formation, and makes its way to the soil surface, where *inter alia* it rapidly loses the flexible condition in which it emerges, and flies away.

THE EGG STAGE

The egg of the carrot fly (fig. 1) is 0.6–0.7 mm. in length and circular in cross-section with a diameter of about 0.15 mm. That end of the egg which is to become the oral end of the embryo is marked by the micropylar cap, a small circular plug with eight sockets around its periphery. The anterior end of the egg-shell is seen in a hatched egg to have incorporated eight lines of weakness along which fractures occur when the larva forces its way out of the egg. Whether this occurs by muscular activity or by physical forces of an imbibitional nature has not been ascertained. The eight "tongues" are freed from their attachments in the plug, which may be seen adhering to the side of the empty egg-shell. (It is interesting to note the similarity between this method of

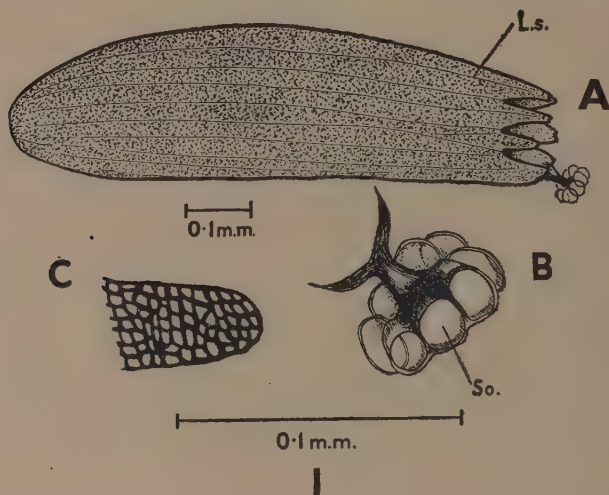


FIG. 1.—A. Hatched egg. B. Micropylar plug. C. Tongue showing sculpturing.

opening of a capsular body and that of the seed capsule in, for example, the bladder campion, *Silene cycubalus*.)

The surface of the egg is sculptured in an irregular reticulate pattern. This extends over the whole surface of the egg, and is superimposed upon longitudinal striations extending meridionally around the length of the egg. Its colour is snow-white; this appears to be due to the action of the surface sculpturing on the light rays rather than to the presence of a pigment. When mounted in a medium of high refractive index, such as canada balsam, the chorion becomes almost wholly transparent.

Fig. 2 shows a balsam mount of an egg in which the embryo has developed almost to the stage of eclosion. Already the different sclerites of the cephalopharyngeal armature are differentiated, as also are the (posterior) spiracles, and their hardening has proceeded almost to completion. Two pairs of sensory papillae are clearly visible on the preoral (head) segment. This embryo establishes the identity of the first-instar larva, as measurements of spiracles and sclerites of the embryo agree with those taken of the smallest instar found free in the soil.

THE LARVAL INSTARS.

As is general among the Cyclorrhapha, there are three larval instars, and their range of length is as follows: first instar 0.6–2.0 mm., second instar 2.0–5.0 mm., and third instar 5.0 to nearly 10.0 mm. The largest larva taken was 9.9 mm. long. Cast skins of the first and second instars have been obtained in the following way from larvae washed out of soil samples. The larvae are

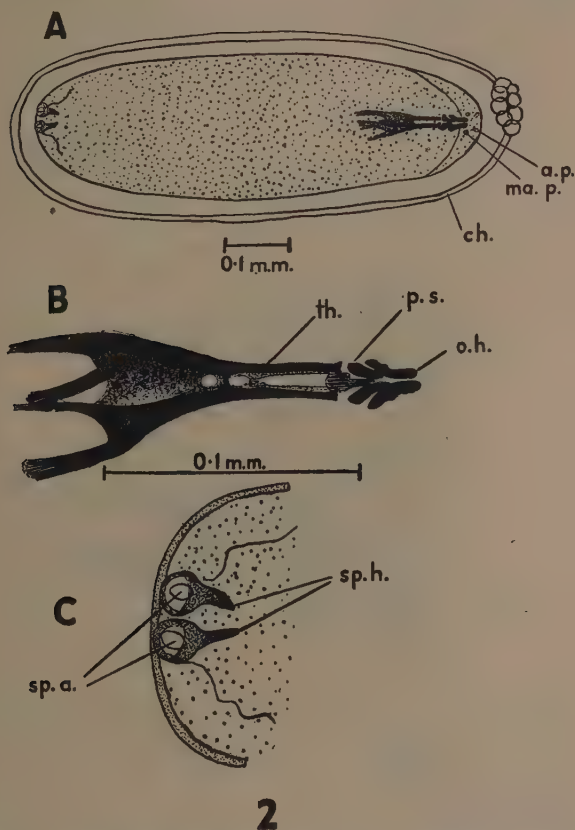


FIG. 2.—A. Egg containing well-developed embryo. B. Cephalopharyngeal skeleton of embryo. C. Posterior spiracles of embryo.

boiled for about half an hour, and then left in a dish of cold water for three to four days. From a larva which in the original sample was ready to moult, the old cuticle and its associated structures can now be dissected off. The newly-freed instar is seen to have the mouth sclerites and spiracles incompletely blackened.

A comparison of the cephalopharyngeal sclerites in the three instars is shown in figs. 3, A and B, and fig. 4. The drawings in fig. 4 are all to the same scale, and sets of measurements have shown that there is very little variation in

the size of the sclerites among different individuals of the same instar. The drawings are from different individuals, but the proportions they represent are typical. All the sclerites present in the third instar can be traced back to the preceding instars.

The left-hand-side posterior spiracles of the three instars are shown similarly in fig. 5. The proportionate length of the spiracular horn changes at the moults, being comparatively insignificant in the third instar. It has been suggested (Smith & Gardner, 1922), that the long horn of the first instar is of service to

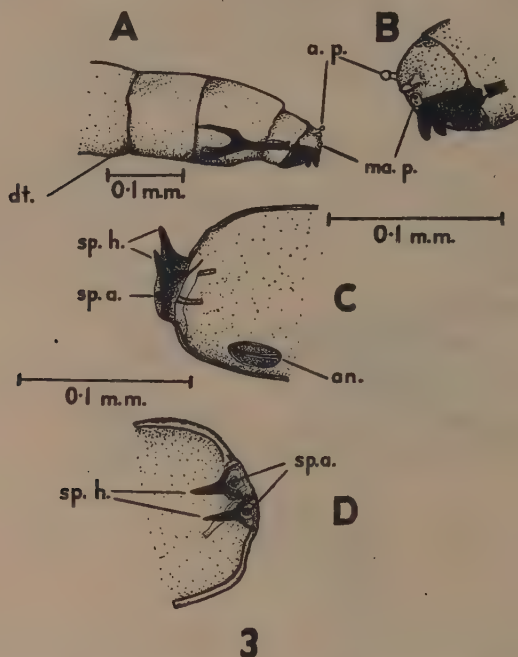


FIG. 3.—Anterior end of first-instar larva. C & D. Posterior end of first-instar larva.

the larva in progressing through the soil. It may also aid escape from the egg, but it persists throughout larval life.

The posterior spiracles increase in size through the three instars, whilst the single respiratory aperture of the first instar is replaced, at the first moult, by triple openings, which are retained at the second moult. The peritreme of the second-instar spiracle shows on its inner border the outer stigmatic scar, denoting the point where the tracheal system was extruded at the first moult. The question of spiracle formation and ecdysis is discussed by Keilin (1944).

Anterior spiracles (fig. 6) are present in the second and third instars, the larva changing from a metapneustic to an amphipneustic state at the first moult.

The number of segments is the same for all instars; a preoral or larval head segment, bearing the antennary and maxillary rudiments, three thoracic, and apparently nine abdominal, making thirteen segments in all.

THE MORPHOLOGY OF THE THIRD-INSTAR LARVA.

The larva is shown from the side in fig. 7, the segments being numbered. It is seen that the anal segment bears the posterior spiracles, and the prothoracic segment the anterior spiracles. The full length of the dorsal tracheal trunk is not shown: only the portions attached to the stigmatic chambers and spiracles. The method of preservation of the specimen had caused the body contents to

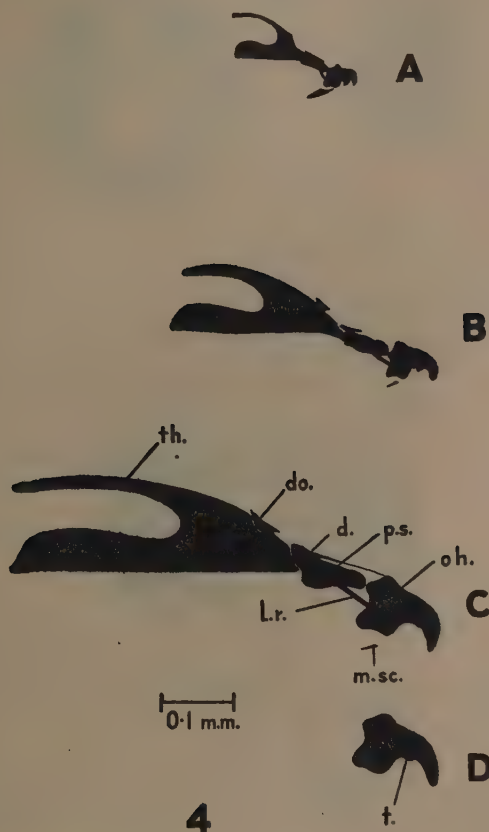


FIG. 4.—A. Cephalopharyngeal sclerites of the first, B. second, C. third instars. D. Aberrant oral hook of same third-instar larva.

contract, drawing the peripheral muscles inwards except at their points of attachment to the cuticle. The anterior margins of abdominal segments 1-7 are beset with cuticular structures in the form of denticles on their ventral surface. These are also found dorsally on the anterior borders of segments 1-3 (fig. 8). These denticles have the toothed projections directed backwards and are locomotory in function. The range of their degree of development is considerable, the two extremes noted in the third instar being given by the two

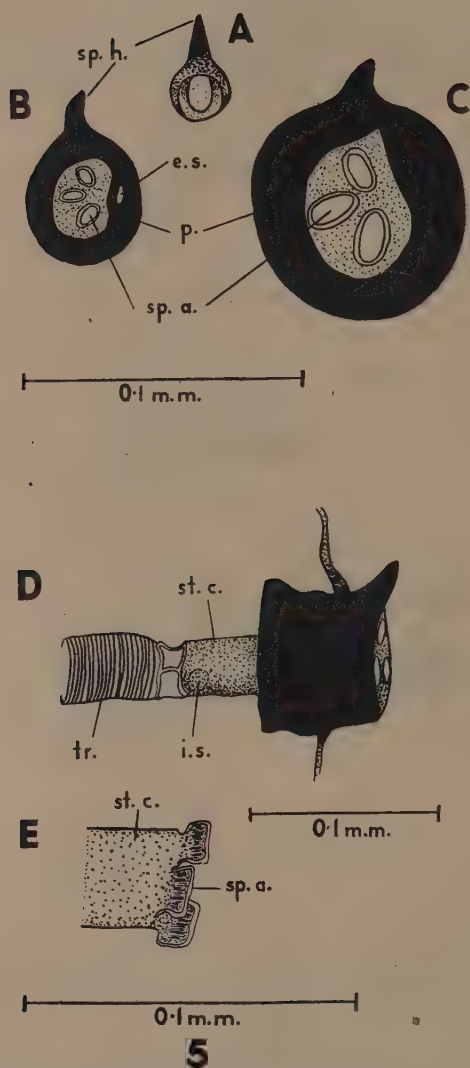
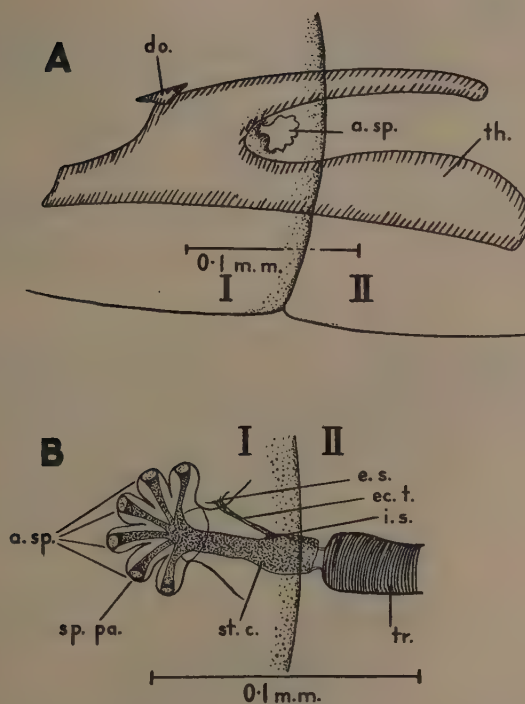
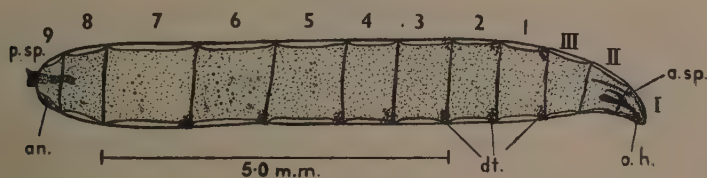


FIG. 5.—Structure of the posterior spiracles of : A. First instar, B. second instar, C. third instar. D. Third instar lateral view. E. Third instar stigmatic chamber.



6

FIG. 6.—Thoracic segments I and II showing A. Anterior spiracle of second instar. B. Anterior spiracle of third instar.



7

FIG. 7.—Lateral view of the third instar.

figures (fig. 8, A and B). Fig. 8, A, shows the less usual development, the denticles being here very thick and mounted on a raised reddish-pigmented

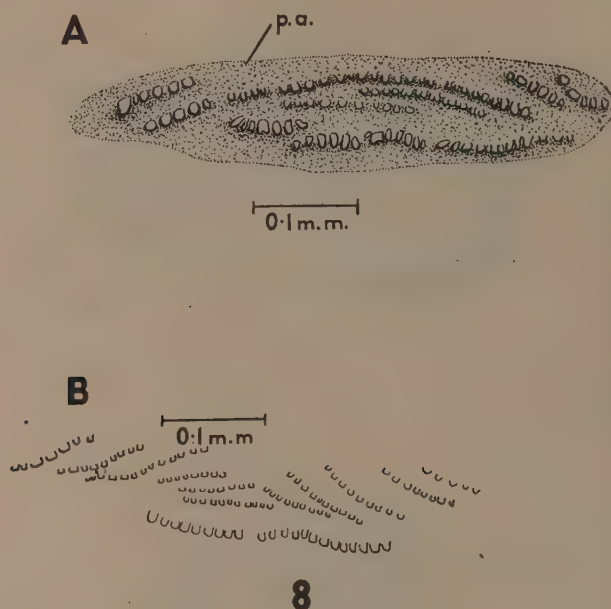


FIG. 8.—Denticles of the third instar showing: A. Extreme development. B. Normal development.

area which stands out clearly from the rest of the body surface. In the earlier instars the denticles are always inconspicuous, though the full number of sets is present.

THE TRACHEAL SYSTEM.

The tracheal system of the third-instar larva from the side and from the dorsal surface is shown in fig. 9. Many of the smaller tracheae and the tracheoles have been omitted. The ventral tracheal system (not figured) is exceedingly complex, consisting of a series of parallel strands running anteriorly, their number increasing from the posterior end forwards as branches are supplied by each segment. The tracheal system exhibits the same metameric differentiation as found by Keilin (1944) for *Drosophila confusa* Staeger, *Acidia heraclei* L., and *Aulacogaster rufitarsus* Macquart. There are ten dorsal commissures and ten ventrally-directed branches from the main dorsal trunks which link up to form the lateral chain of metameric units conspicuously shown in the holo-, peri-, or hemipneustic systems. The ten metameres correspond to the pro- and metathoracic segments, and to the eight abdominal segments. The 8th and 9th (anal) segments correspond to one tracheal segment and branch only. There is no external evidence of the metameric break (such as an

enlargement of the trachea) but microscopically the breaks in the taenidial lining can be seen; these are not quite smooth patches, as some ridging of the lining does occur (see fig. 10).

In the mature larva can be seen the vestiges of the primitive spiracular system, such as is found among the BIBIONIDÆ, and the spiracles representing the peripneustic system are retained in a non-functional condition in the carrot fly larva. They are present as small depressions of the larval cuticle and from these, thin tracheal connections with the lateral tracheal system exist. The

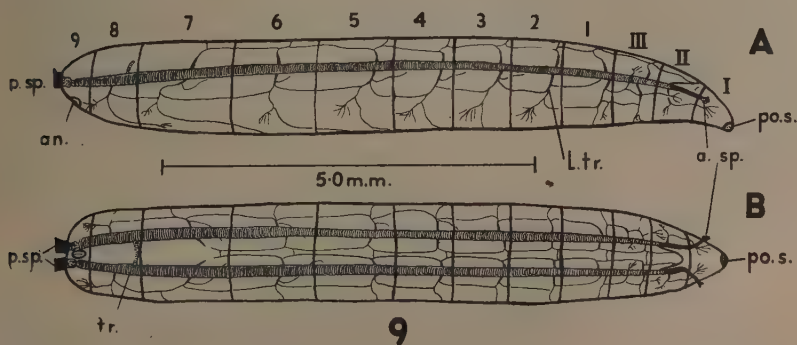


FIG. 9.—Tracheal system of the third-instar larva. A. Lateral view. B. Dorsal view.

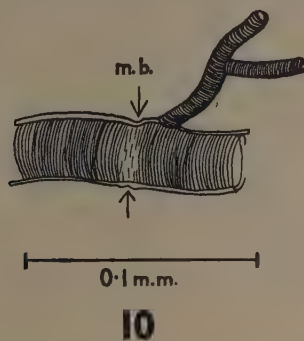


FIG. 10.—Dorsal tracheal trunk of third-instar larva showing metameric break in taenidial lining.

vestiges of this spiracular system are best seen in a stained preparation of the membranous sheath lying between the puparial and pupal cuticles after the formation of the pupa. The non-functional spiracles then appear as slight annular thickenings at the distal end of the solid tracheal strand joining them to the functional branches of the lateral tracheae.

The first tracheal metamere of the dorsal longitudinal trunks is more heavily thickened and more rigid than the succeeding ones (figs. 9 and 18). This may be connected with the function it probably performs during early metamorphosis.

The paired anterior spiracles of the third-instar larva occurring on the posterior border of the prothoracic segment are typical in form (fig. 6). Each consists of an external palmate cuticular projection, with 5, 6, or 7 branches or lobes. Each lobe opens separately to the air and is connected to one of the branches from the stigmatic chamber. The lining of these branches seems identical with that of the inner part of the chamber; hairs or bristles do not appear to be present. The stigmatic chamber joins the dorsal tracheal trunk by a narrowed neck, devoid of the roughening of the chamber itself and possessing no taenidial lining like the trachea. A short distance anterior to this junction the shrunken ecdysial sheath of the previous instar's tracheal system may be seen as a transparent unsculptured thread. This extends from the base of the stigmatic chamber to the cuticle of the larva where its point of insertion marks the place of the extrusion of the anterior stigmatic chamber and of the tracheae of the previous instar. A similar structure exists in connection with the posterior spiracles of the third instar, but here the cuticular point of insertion of the ecdysial sheath is less easily traced, as it occurs on the inner surface of the black peritreme of the spiracle. The scar at the base of the stigmatic chamber is more obvious (fig. 5). (The position of the outer scar is clearly seen in the second instar.)

THE CEPHALOPHARYNGEAL SCLERITES.

The armature of the mouth (fig. 4) consists of a number of paired and unpaired sclerites. The mode of feeding is the same for all the instars and there is constancy of function of the various sclerites during larval life.

The most anterior sclerites are the paired, oral hooks or mandibular sclerites, which are hollow, and which articulate with the parastomal sclerites. These are attached posteriorly to the thecal sclerites, which anchor the whole armature in the body of the larva and partly ensheath the pharynx and pharyngeal muscles. The sclerite between the thecal sclerites and the oral hooks, formerly called the hypostomal sclerite, consists of paired lateral parastomal sclerites connected by a median hypostomal arch (Miller, 1932). Other sclerites are: a dorsal sclerite above the anterior end of the thecal sclerites (fig. 4 do), a smaller dorsal sclerite over the hypostomal arch (d), paired lateral rod-like sclerites connecting and overlying laterally the mandibular and parastomal sclerites, and the central dentate sclerite situated within the muscular mass ventrally to the posterior end of the oral hooks. In *Psila* the dentate sclerite does not appear to consist of two fused sclerites, such as were found by Miller in the larva of *Calliphora quadrimaculata* Swed.

Further details of the right-hand-side oral hook and of the articulating part of the parastomal sclerite are shown in fig. 11. The oral hook articulates by a condyle with the parastomal sclerite and has a lateral projection (L). The main points of muscle insertion (M), as dictated by the function of the sclerite as a vertically-moving jaw, lie dorsally and ventrally. The parastomal sclerite has a projecting shelf (S) on the distal side; attached to this, and lying dorsal to the lower external projection (L) of the oral hook, is the lateral rod, prolonged anteriorly as a fibrous extension. This sclerite appears to be directly attached to the shelf of the parastomal sclerite at (Z).

The great majority of the third-instar larvae examined had only a single smooth tooth on the oral hook, but in six larvae this sclerite had the structure shown in fig. 4, D, having a small vestige of a tooth on the inner edge. The significance of this abnormality is not apparent.

THE MUSCULATURE OF THE BUCCAL ARMATURE AND ITS MODE OF ACTION.

The musculature can be divided into two main groups: those muscles attached at both ends to the chitinous sclerites, and those attached between the sclerites and other parts of the larva. These may be designated the intrinsic and extrinsic groups respectively.

The intrinsic muscles are given in fig. 12, A, and consist of a dorsal muscular band (d.m.b.) extending from the oral hook to the hind end of the dorsal horn of the thecal sclerite, and uniting the two symmetrical halves of the whole armature. This band also incorporates the two dorsal accessory sclerites, do and d (see fig. 4, C). The latter has an anterior prolongation which extends to the point of muscle attachment on the posterodorsal edge of the oral hook. The function of these muscles may be partly that of retracting or elevating the

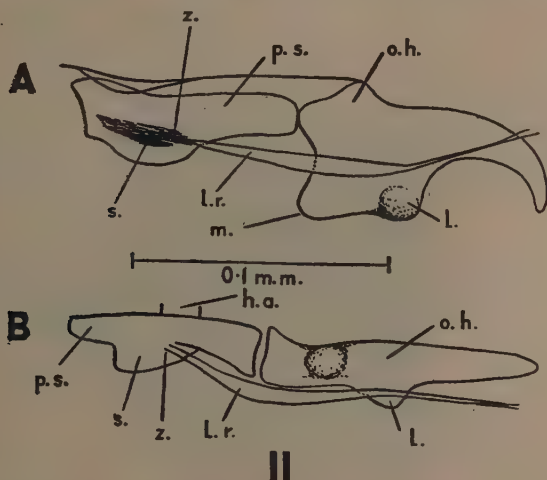


FIG. 11.—Oral hooks and parastomal sclerites of the third-instar larva. A. Lateral aspect. B. Dorsal aspect.

hook. This action is duplicated by the narrow muscle (ei) extending from the posterodorsal angle of the oral hook to the ventral horn of the thecal sclerite, where it is attached laterally and externally.

The other chief muscles of the intrinsic group are the two more ventrally placed muscles (di and di') extending from the posteroventral angle of the oral hook to the external face of the ventral horn of the thecal sclerite, and overlying the small elevator muscle. These muscles act as depressors of the oral hook. The intrinsic musculature as a whole would seem to serve also as a tensor system to facilitate the action of the extrinsic muscles.

The extrinsic muscles are shown displayed in fig. 12, B; the pharynx and its associated dilator muscles are represented as an undifferentiated mass. Attached to this mass are a protractor muscle (p.e.) and a smaller muscle (e.e.) which pass anteriorly to the posterodorsal angle of the oral hook. Ventrolaterally two muscles (d.e. and d.e'.) pass forwards over the intrinsic muscles to the posteroventral angle of the oral hook, where their insertion is partly on the outer

and partly on the ventral face of that sclerite. These muscles serve also as depressors of the oral hook.

Attached to the dorsal cornua of the thecal sclerites are the main protractor muscles (*p.e.* and *p.e''*), one pair extending laterally and the other dorsally. The main depressors of the oral hook are shown in fig. 12, B, and fig. 13 as

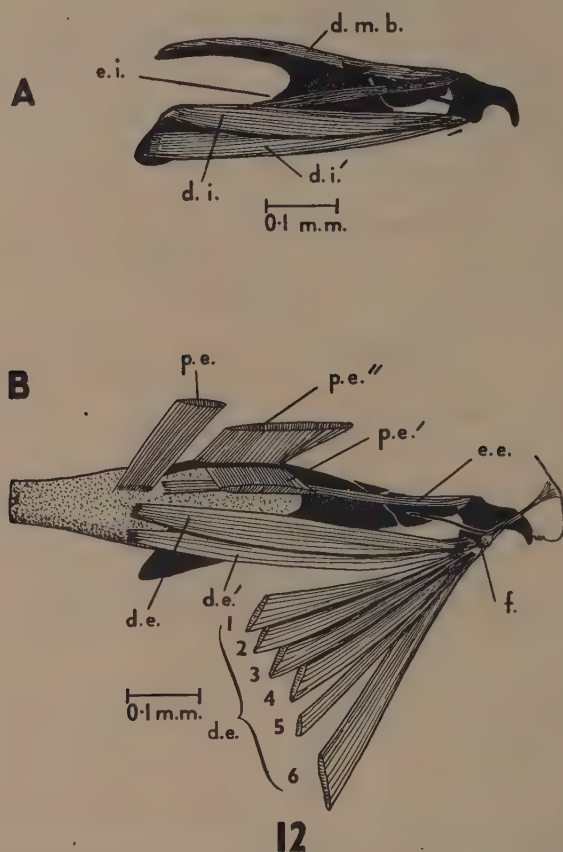


FIG. 12.—The muscles of the buccal armature. A. The intrinsic muscles. B. The extrinsic muscles.

d.e. 1-6. These muscles are attached at their posterior ends to the ventral body-wall musculature, and anteriorly to the fibrous-muscular band (*f*).

Also embodied in these muscles are the rod-like lateral sclerites which pass forwards from the parastomal sclerite. Embedded in the fibrous band directly ventral to the point of insertion on the oral hook is the median dentate sclerite. This, in conjunction with the fibrous band itself, gives rigidity and unity of action to these ventral muscles, which function in concert. The lateral disposition of the more external of these muscles is shown in fig. 13, and the lateral rod is seen to be continuous at its anterior end with the tissue of the larval head

segment, passing in a dorsal direction almost completely over the oral hook. The preoral (head) segment also appears as a continuation of the fibrous band, and the opening in its median plane is the mouth through which the oral hooks are extruded.

From the morphological arrangement of the muscles an attempt will be made to describe the functioning of the various parts of the buccal armature.

The carrot fly larva feeds by rasping away small portions of the root tissue by vertical downward strokes of the oral hooks, the food then being transferred

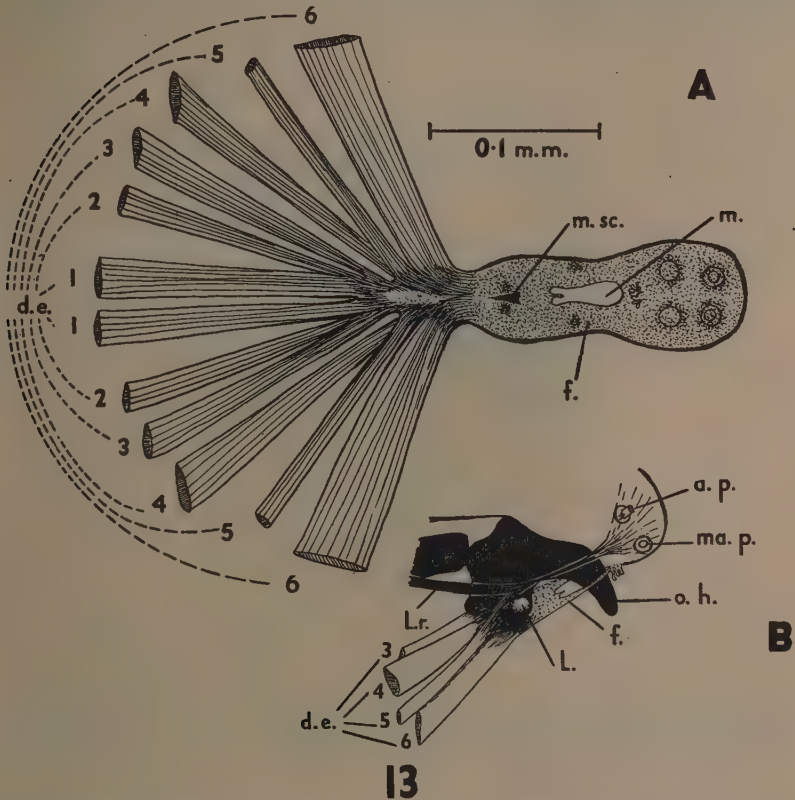


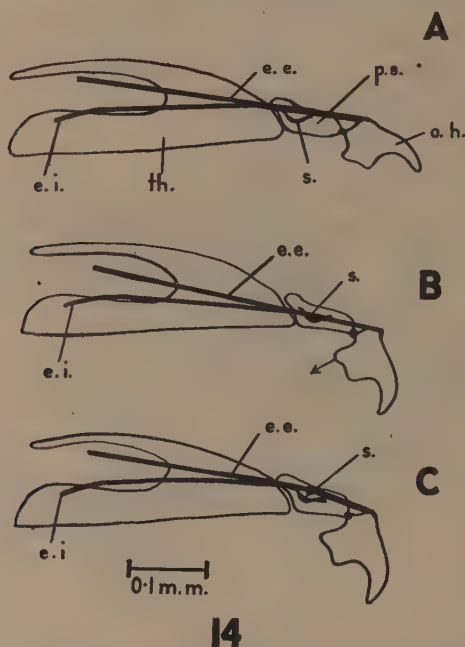
FIG. 13.—Main depressor muscles of the oral hooks. A. Vertical aspect. B. Lateral aspect.

to the pharynx. This movement is plainly observable in living larvae, and the biting stroke may be used as an accessory means of locomotion. The larva obtains a grip on some object with the exposed teeth of the oral hooks, and then pulls the whole body forward towards this point of adherence.

The main muscles causing the downward stroke are those of the ventral depressor group, embodying the dentate sclerite. When these muscles contract the oral hooks are swung downwards, and the teeth protrude. The preoral segment is pulled simultaneously backwards and upwards by its connection with the muscles through the lateral rod-like sclerites. These sclerites also help

to prevent the oral hooks from diverging widely when driven into the food. The mechanism is thus seen to be partly cam-like, the sliding surfaces involved being the curved dorsa of the oral hooks and the front edge of the mouth opening.

The elevation of the oral hooks is accomplished by the elevator muscles of the intrinsic and extrinsic systems, see fig. 14 (e.i. and e.e.). It will be seen that when the hooks are fully depressed, the line of action of these two muscles would be expected to pass very close to the fulcrum of the articulation of the oral and parastomal sclerites. This would seriously diminish the moment of these muscles and render them almost incapable of performing the action of elevation.



14

FIG. 14.—The mechanics of the elevation of the oral hooks. A. Oral hook retracted, elevator muscles contracted. B. Oral hook protracted, elevator muscles relaxed. C. Oral hook being retracted by elevator muscles.

However, these muscles both pass dorsally to the lateral shelf on the parastomal sclerite, and this arrangement maintains their moment about the fulcral point at an effective value. Fig. 14, C, shows the interference of the shelf, acting as a pulley in the transmission of the tension.

The action of the muscles may be summarised by outlining the mode of feeding. The thoracic segments and the mouth armature are protracted into contact with the food, the oral hooks being in the elevation position. These are then driven into the food by the powerful depressor muscles, and at the same time the mouth gapes widely open. The whole armature is then retracted, the food passes into the pharynx, and is held by the ventrally-pointing oral teeth. The elevator muscles then swing the oral hooks dorsally in preparation

for the next bite, and the food is dealt with by the muscles of the pharynx. Retraction and ingestion appear to be effected by the action of the ventral group of muscles, following the relaxation of the protractors of the whole armature.

THE SENSORY APPARATUS OF THE LARVA.

The sensory apparatus of the third-instar larva is shown in fig. 15 and partly in fig. 13, and of the first-instar larva in fig. 3; it is essentially the same for all instars. The apparatus consists of two pairs of papillae, the anterior or antennary and the posterior or maxillary. The maxillary papillae appear to

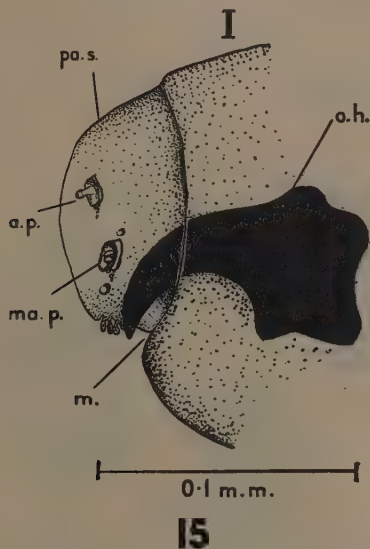


FIG. 15.—Head segment of third-instar larva showing sensory papillae.

represent the palpi of the Nematoceran maxillae (Imms, 1938). Lateral sense organs are found in the pharynx around the oral opening. The function of the papillae is not known, and has not been experimentally investigated either in the carrot fly larva or to any great extent among the Cyclorrhapha.

THE STRUCTURE OF THE PHARYNX.

The structure of the pharynx of the third-instar larva is shown in fig. 16 by transverse sections at three different regions. The floor of the pharynx is smooth, without the ridges or "côtes" which characterise the saprophagous forms of the larvae of the Cyclorrhapha. This condition agrees with the findings of Keilin (1912). The basket-like structure of the pharyngeal sclerites is also shown, together with the muscles dilating the pharynx. The latter are arranged partly oblique to the plane of section and consequently appear as fragments only. Ventrally the two pharyngeal sclerites are joined; this union is chitinous and probably flexible.

THE PUPARIUM AND METAMORPHOSIS.

When fully fed the larva of the third instar changes directly into the puparial stage (fig. 17). The larva shrinks and alters its proportions, shrinkage at the anterior end being greater than at the posterior. The larval cuticle is thrown into folds which appear as rings or partial rings on the puparium, and the creamy whiteness of the larva changes to a paler or darker golden brown. The denticles of the larva can be seen on the puparium and the anal opening is more conspicuous than formerly.

The head and prothoracic segments of the larva are drawn into the cavity

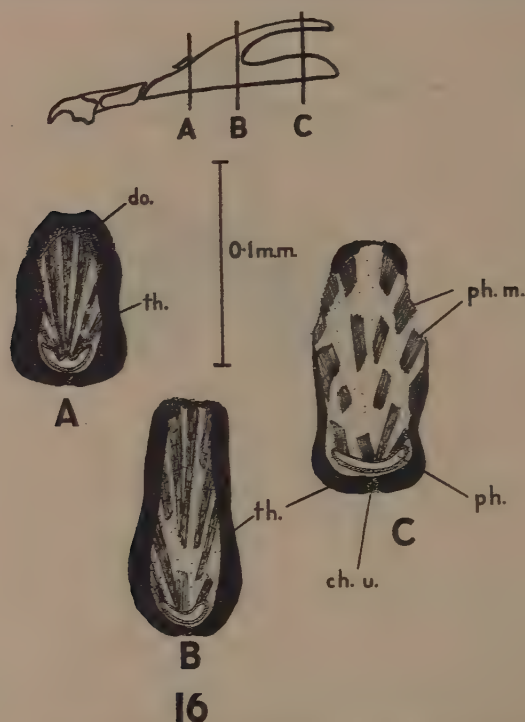
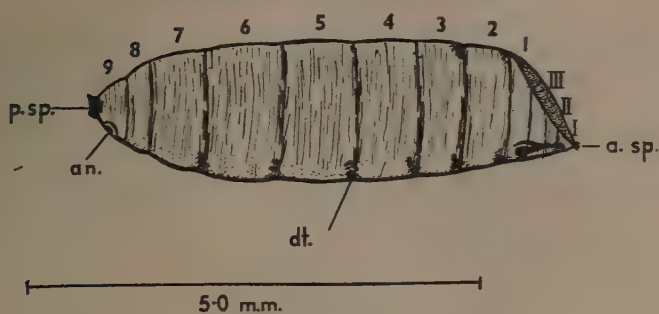


FIG. 16.—Transverse sections of the pharynx of the third-instar larva.

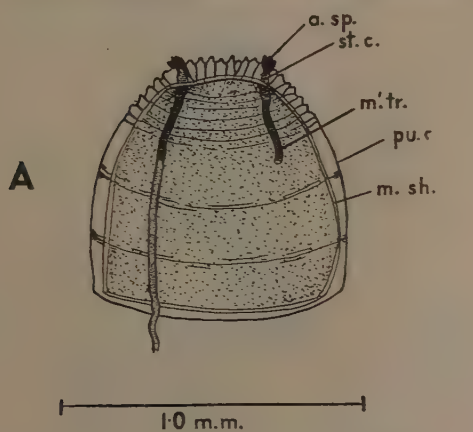
of the puparium, and as a result the anterior larval spiracles come to lie at the extremity of the puparium. The dorsal part of the meso- and metathoracic segments and of the first abdominal segment sinks in and the demarcation of the line of rupture of the "lid" of the puparium takes place.

The stigmatic chamber and the prothoracic metamere of the dorsal tracheal trunk remain attached to the spiracles and retain their shape; beyond the first metameric break the trachea is collapsed. The posterior spiracles also retain connection with their stigmatic chambers. The remains of the rest of the longitudinal tracheal system are seen as a tangled mass of collapsed tubes lying dorsally to the contents of the puparium (fig. 18). The non-functional

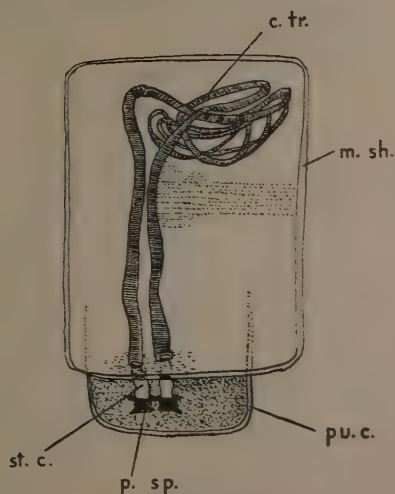


17

FIG. 17.—Puparium of the Carrot Fly, lateral view.



B

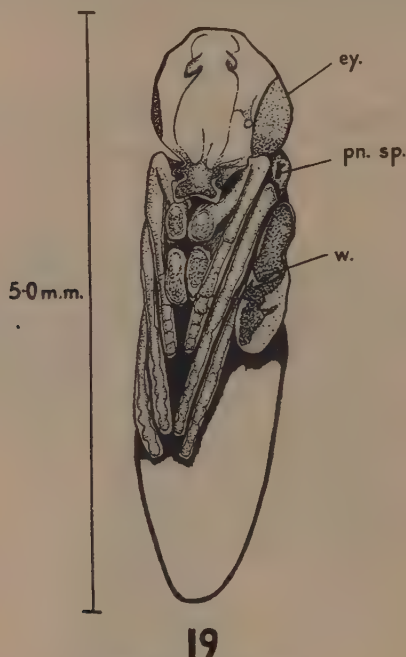


18

FIG. 18.—Tracheal relations at the ends of the puparium. A. Anterior end. B. Posterior end.

lateral spiracles of the larva do not leave any trace of their position on the puparium itself (cf. Snodgrass, 1924, for *Rhagoletis pomonella* Walsh), but their presence on the inside of the membrane lining the puparium has been mentioned above.

When fully formed, the pupa of the carrot fly can be seen through the semi-transparent puparial wall and through its lining membrane. The outline of the adult can be traced, as in fig. 20, which shows the pupa in bare outline, and as in fig. 19 which shows a pupa at an advanced stage of development; here the segmentation of the adult legs inside the pupal cuticle has already begun. The



19

FIG. 19.—The pupa.

surface of the pupal head is covered with fine regularly placed denticles, *i.e.* it is shagreened (see fig. 20).

The leg and wing sacs are present as extensions of the pupal cuticle and do not adhere along their length to the body of the pupa. Inside these sacs differentiation of the adult appendages takes place. Fig. 21, A, shows a transverse section of an advanced pupa still enclosed in the puparium and the membranous sheath; the leg and wing sacs contain the already differentiated adult forms. Enlarged sections of the metathoracic leg, and the lateral tracheal remains attached to the membranous sheath, are also shown (fig. 21, B). The leg section is at the base of the tibia, and the fragmented bristles appear as dark rods in the space between the adult and the pupal cuticles. The macrotrichia of the wings can already be seen in the folds formed by the crumpling and compressing of the wing in the wing sac.

The respiratory system of the pupa consists of paired pronotal spiracles and

an associated tracheal system, part of which is shown in fig. 20, A. The spiracles bear the same morphological relationship to the anterior spiracles of the third-instar larva as do the latter to the anterior spiracles of the second-instar larva. The ecdysial sheath or tube with the inner and outer stigmatic scars are visible here as in the later larval instars. The structure of the pronotal

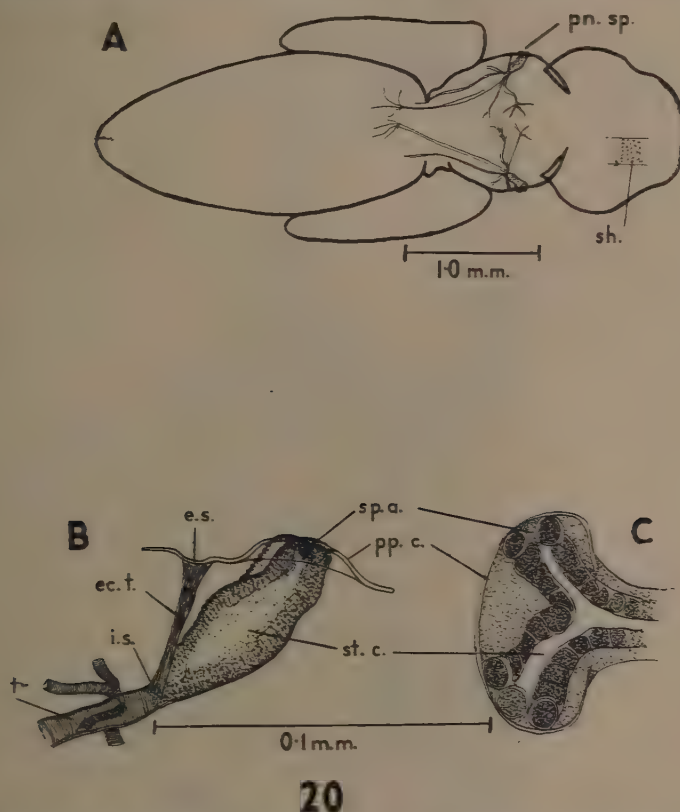


FIG. 20.—The pronotal spiracles of the pupa. A. Position of the pronotal spiracles of the pupa. B. Spiracle in vertical longitudinal section. C. Spiracle in horizontal section.

spiracle is shown in two longitudinal sections at right angles to each other (fig. 20, B and C). Instead of the more numerous papillae of the larval prothoracic spiracles, two only are present and are more massive in proportion. The stigmatic chamber appears little different in structure from that of the third-instar larva.

The subject of pupal spiracles is extensively dealt with by De Meijere (1902).

THE PUPARIAL COMPLEX.

If from a puparium containing a well-developed pupa, as in fig. 19, the anterior end is dissected away as far back as the second abdominal segment of

the larva, the anterior spiracles with their attached portion of the tracheae, and the cephalopharyngeal sclerites of the larva, usually come away with it. The pupal head is then exposed, and the pupa may be withdrawn from the

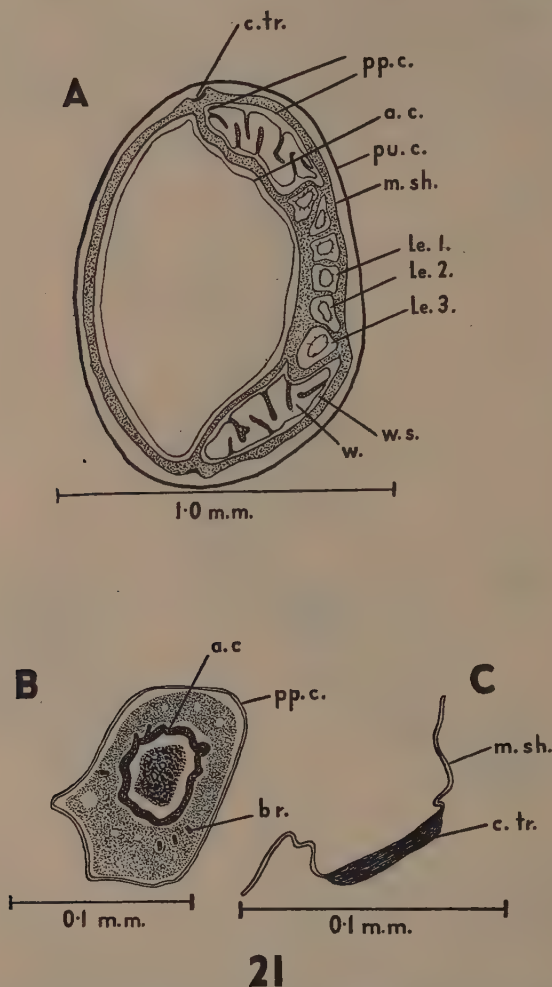


FIG. 21.—Structure of the advanced pupa. A. Transverse section through whole body inside puparium. B. Transverse section of metathoracic leg. C. Membranous sheath with lateral tracheal remains.

puparium together with the membranous lining of the puparium. The lateral and dorsal remains of the larval tracheal system are then seen to lie inside this membrane (fig. 21, C). The cephalopharyngeal sclerites and the pharynx are also attached internally to the membrane, the anterior and posterior ends of which are pierced by the stigmatic chambers of the larval spiracles (fig. 18).

The pharyngeal structures and also the hind-gut are morphologically continuous with this membrane. There is no well-defined surface sculpturing of the membrane, only a rather inconspicuous dotting, and a section shows it to be only about $1\ \mu$ thick and apparently structureless. Within the membrane the pupa lies entirely free, there being no observable point of attachment.

The presence of this membranous sheath has been recorded so far in only a few Diptera and has been the subject of some discussion.

Snodgrass (1924) says that the larva of *Rhagoletis pomonella* Walsh changes into an intra-puparial fourth-instar larva instead of directly into a pupa . . . "a larval stage complete in all respects except for the retention of the stomodeal, proctodeal, and tracheal linings of the third larval instar." The cuticle of this instar is the membranous sheath described for the carrot fly. In *Rhagoletis* Loew this postpuparial instar moults to form the true pupa which then lies inside the puparial capsule and also inside the membranous sheath, the latter marked by a close-set papillation.

The sheath was also noted by Kunckel d'Herculais (1875-81), but Lowne (1892) did not recognise the separate membrane in *Calliphora erythrocephala* Meigen, stating that the extruded intima of the great longitudinal tracheal trunks lies directly inside the puparial case. Miall and Taylor (1907) say of *Phytomyza aquifolii* Goureaux that "the pupa, shrouded in a delicate transparent membrane (the true pupal skin), remains enclosed in the larval cuticle." Hewitt (1908) gives an account of the pupation of *Musca domestica* L. substantially similar to Lowne's for the blowfly *Calliphora* Robineau-Desvoidy, whilst Irwin-Smith (1923) has described the method of pupation of *Metoponia rubriceps* Macquart (STRATIOMYIDAE). In the latter three skins were observed to be present on the ripe pupa, the "pupa case, pupa sheath, and epidermis of the imago, representing three distinct ecdyses." These are supposed to correspond to the three stages of pronymph, nymph and imago as described by Lowne. He considers the pronymph as the stage at which the head and thoracic appendages are still invaginated and the larval organs are undergoing histolysis; the larval skin having been shed to form the puparium, and the body enclosed in a temporary membrane, the paraderm. Irwin-Smith says of the pronymph: "The pupa sheath is not yet formed, and the body is still covered with an integument, the external layer of which consists of a thin transparent membrane. Whether this membrane is the paraderm of Lowne or the pupal ectoderm, there is not sufficient evidence to prove."

This investigation of the puparial complex of the carrot fly has provided little new evidence for the correct interpretation of the origin and nature of the membranous sheath. In the carrot fly the pupa is surrounded by two complete membranes, the membranous sheath and the puparium. The presence of remains of the dorsal tracheal trunk of the larva inside the membranous sheath would appear to indicate an incomplete moult to form the membranous sheath, the tracheal lining being extruded only at the formation of the pupa. The observations of Snodgrass on the time relations of development inside the puparium and the structure of the membranous sheath point to there being a distinct instar, albeit much suppressed. It is possible that the membrane may have a certain functional significance. Thompson (1929), discussing the Muscoid Diptera, says: "The morphogenesis of the puparium seems principally to depend on (1) the contraction of the larva, from which results (2) an increase in the hydrostatic pressure of the coelomic fluids, and (3) on the detachment of the hypodermis, associated with (4) a degeneration of the integumental muscle fibres: there thus results a regular ellipsoidal form, with a smooth surface,

which is fixed by the transformation of the larval integument into a hard and rigid shell." It seems possible that the membranous sheath, whatever its homologies, fits into Thompson's scheme of morphogenesis by acting as the resister and distributor of pressure within the young puparium, thus evening out the grosser irregularities in the larval cuticle. The presence of ridging or folds in the larval cuticle on the mature puparium shows that the process of puparium formation is not *simply* one of contraction and hardening. More investigation of the matter is needed, especially concerning the exact time of formation of the membrane in relation to the hardening of the larval cuticle. The extrusion of the pupal spiracles in *Paraspinophora maculata* Meigen through positions already determined in the larval cuticle (Keilin, 1944) indicates a very close connection between the third-instar larval and the pupal stages.

THE RESPIRATION OF THE PUPA.

The anterior metamere of the dorsal tracheal trunk of the third-instar larva (fig. 18) passes through the membranous sheath surrounding the pupa and acts as a communication channel between the cavity of the sheath and the outer air (via the prothoracic spiracles and stigmatic chambers forming part of the anterior end of the puparium). The space between the pupa and the membranous sheath is, in the carrot fly, usually gas-filled, and the apertures of the pupal pronotal spiracles open into the gas-filled space. The membranous sheath is gas-tight, and the rigid tracheal metamere is probably the means of entry of the gas.

It would be of considerable interest to observe the structure and the relations within the puparium of the anterior part of the larval tracheal system in those Diptera in which protrusion of the pronotal spiracles of the pupa into the outer air takes place.

SUMMARY.

1. The carrot fly larva investigated is that of *Psila rosae* Fabricius.
2. The life history is typical of a root-feeding phytophagous Dipteron, the eggs being laid in the soil near the host; the larvae on hatching enter the host and feed thereon until puparium formation. Moulting probably occurs when the larva is free in the soil. The puparia are found in the soil, and the fly emerges underground.

3. The egg of the carrot fly is sub-cylindrical, and measures 0.6–0.7 mm. long and 0.15 mm. in diameter; it is snow-white in colour. The pre-eclosion embryo can be seen through the chorion in prepared specimens, and is identical with the youngest larva taken from hosts or from the soil. Morphological evidence for three larval instars is provided by the production of artificial "moult" in the laboratory.

The size range in length of the larval instars is as follows: first instar 0.6–2.0 mm., second instar 2.0–5.0 mm., and third instar 5.0–9.9 mm.

Anterior (prothoracic) spiracles are lacking in the first-instar larva but are present as palmately lobed projections of the cuticle in the second and third instars. The posterior or anal spiracles have each a single aperture in the first instar, and a triple aperture in the later instars.

4. The larva consists in all instars of a preoral (head) segment, three thoracic, and nine abdominal segments. The last are, however, supplied by only eight branches from the dorsal tracheal trunks.

The anterior borders of abdominal segments 1-7 are beset with cuticular denticles on the ventral surface, and abdominal segments 1-3 are similarly equipped on the dorsal surface. These denticles occur in all instars, but are only conspicuous in the third instar, where they may be associated with a reddish pigment.

5. The tracheal system of the third-instar larva consists of ten metameres, two thoracic and eight abdominal, the mesothorax being devoid of any individual tracheal metamere. The larva is amphipneustic in the third and second instars. The remainder of the primitive peripneustic system persists as a metameric lateral tracheal system and the vestigial spiracles of the other metameres are connected to the lateral system by functionless tracheal branches. The functional spiracles each open into a stigmatic chamber, and at the base of this can be seen (especially in the third instar) the inner stigmatic scar, indicating where the ecdysis of the previous instar's tracheal system took place. The path of this extrusion is marked by the ecdysial tube and the outer stigmatic scar.

6. The buccal armature consists of paired oral hooks, thecal sclerites, parastomal sclerites connected by a median hypostomal arch, and various associated accessory sclerites. The musculature and mode of action of these sclerites are described.

The head (preoral) segment of the larva bears antennary and maxillary sensory papillae, the functions of which are not known. Laterally-placed sense organs also occur in relation to the pharynx. The pharynx itself is "smooth," without the ridging found in the saprophagous *Cyclorrhaphous* larvae.

7. Visible metamorphosis begins by a contraction and hardening of the third-instar larval cuticle to form the puparium. This, together with its contents, has been designated the "puparial complex." Internally to the cuticular outer layer of the puparium is a thin membranous sheath, to the inside of which adhere the remains of the tracheal system of the third-instar larva. Within these two layers is the pupa proper with its own cuticle, and inside this the differentiation of the imaginal cuticle and the imago takes place.

8. The pupa has a separate tracheal system, developed directly in relation to that of the third-instar larva. Respiration of the pupa is apparently accomplished through a gas-filled space lying between the pupa and the membranous sheath. Into this space the pronotal spiracles of the pupa open.

ACKNOWLEDGMENTS.

The authors are indebted to the Agricultural Research Council for a grant which has financed the whole investigation on Carrot Fly during the years 1940-45, to Dr. W. H. Thorpe (Zoological Laboratory, Cambridge) and Mr. G. P. Hirsch (School of Agriculture, Cambridge) for kindly reading and criticising the proofs.

REFERENCES.

- DE MEIJERE, J. C. H., 1902, Ueber die prothoracal Stigmen der Dipteren Puppen. *Zool. Jb.* 15 : 623.
 D'HERCULAI, K., 1875, *Recherches sur l'organisation et le développement des Volucelles, insects diptères de la famille des Syrphides*. Paris.
 HEWITT, C. J., 1908, The structure, development and bionomics of the House Fly, *Musca domestica* Linn. *Quart. J. Micr. Sci.* 52 : 495.
 IMMS, A. D., 1938, *Text book of Entomology*. London.

- IRWIN-SMITH, V., 1923, Studies on the life histories of Australian Diptera Brachycera. Part I. STRATIOMYIDAE. The respiratory system in the larva, pupa and imago of *Metoponia rubriceps* Macquart. *Proc. Linn. Soc. N.S. Wales* **48** : 49.
- KEILIN, D., 1912, Structure du pharynx en fonction du régime chez les larves de Diptères Cyclorrhaphes. *C.R. Soc. Biol.* **155** : 1548.
- , 1944, Respiratory systems and respiratory adaptations in larvae and pupae of Diptera. *Parasitology* **36** : 1.
- LOWNE, B. T., 1892, *The anatomy, physiology, morphology and development of the Blow-fly (Calliphora erythrocephala)*. London.
- MIALL, J. C., and TAYLOR, T. H., 1907, The structure and life history of the Holly Fly (*Phytomyza aquifolii*). *Trans. ent. Soc. Lond.* **1907** : 259.
- MILLER, D., 1932, The bucco-pharyngeal mechanism of a Blow-fly larva (*Calliphora quadrimaculata*). *Parasitology* **24** : 491.
- PETHERBRIDGE, F. R., and WRIGHT, D. W., 1943, Further investigations on the biology and control of the Carrot Fly (*Psila rosae* F.). *Ann. appl. Biol.* **30** : 248.
- SMITH, K. M., and GARDNER, J. C. M., 1922, *Insect Pests of the Horticulturist*. London.
- SNODGRASS, R. E., 1924, Anatomy and Metamorphosis of the Apple Maggot, *Rhagoletis pomonella* Walsh. *J. agric. Res.* **28** : 1.
- THOMPSON, W. R., 1929, A contribution to the study of morphogenesis in the muscoid Diptera. *Trans. ent. Soc. Lond.* **77** : 195.

REFERENCE KEY TO FIGURE LABELLING.

a.c.	adult cuticle.
an.	anus.
a.p.	antennary papillae.
a.sp.	anterior spiracle.
br.	bristles of the adult leg, fragmented.
c.tr.	collapsed tracheae.
ch.	chorion.
ch.u.	chitinous ventral union of thecal sclerites.
do.	posterior accessory dorsal sclerite.
d.	anterior accessory dorsal sclerite.
d.e. 1-6.	main depressor muscles of oral hooks, extrinsic.
d.e.	other depressors of oral hooks, extrinsic.
d.i.	depressors of the oral hooks, intrinsic.
d.m.b.	dorsal muscle band, intrinsic.
dt.	denticles of the larval cuticle.
e.e.	elevator muscles of the oral hooks, extrinsic.
e.i.	elevator muscles of the oral hooks, intrinsic.
ect.t.	ecdysial tube or sheath.
e.s.	external stigmatic scar.
ey.	eye of adult visible through pupal cuticle.
f.	fibrous band co-ordinating d.e. 1-6.
h.a.	hypostomal arch.
i.s.	internal stigmatic scar.
l.	lateral projection of oral hook.
le 1, le 2 and le 3.	legs of the adult ensheathed in pupal cuticle.
l.r.	lateral rod-like accessory sclerite.
l.s.	longitudinal striations of the egg.
l.tr.	lateral tracheal branches.

m.	position of muscle insertions on the mandibular sclerite.
m. l. tr.	first tracheal metamere, rigid.
m.	mouth.
m.b.	metameric break in the tracheal system.
m.s.	membranous sheath surrounding the pupa.
ma.p.	maxillary sensory papilla.
m.sc.	median (dentate) sclerite.
o.h.	oral hook.
p.	peritreme of posterior spiracle.
p.a.	pigmented area surrounding cuticular denticles.
p.e.	protractor muscles of extrinsic group.
p.s.	parastomal sclerite.
p.sp.	posterior spiracle.
ph.	pharynx.
ph.m.	pharyngeal dilator muscles.
pn.sp.	pronotal spiracles of the pupa.
po.s.	preoral (head) segment.
pp.c.	pupal cuticle.
pu.c.	puparial cuticle (larval cuticle after hardening).
s.	shelf on parastomal sclerite.
sh.	"shagreening" of pupal head.
so.	socket in micropylar plug.
sp.a.	spiracular aperture.
sp.h.	spiracular horn.
sp.pa.	spiracular papilla.
st.c.	stigmatic chamber.
t.	accessory aberrant tooth on oral hook.
th.	thecal sclerites.
tr.	tracheal trunk.
w.	wing.
w.s.	wing sac, of pupal cuticle.
z.	point of attachment of lateral rod to parastomal sclerites.
I, II, III.	thoracic segments of larva.
1-9.	abdominal segments of larva.

Vol. 97. Part 15. Pp. 381-404, 6 figs.

15th November, 1946.

IMP. INST. ENT.

LIBRARY

21 NOV 1946

Em. 344

THE

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

CHEN, Sicien H. Evolution of the insect larva . . . 381-404, 6 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D. }

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

EVOLUTION OF THE INSECT LARVA

By Sicien H. CHEN.

(National Institute of Zoology, Academia Sinica, China.)

Communicated by Dr. A. D. Imms, F.R.S.

(WITH SIX TEXT-FIGURES.)

Manuscript received 10th January, 1946.

(Read 5th June, 1946.)

CONTENTS.

	PAGE
Introduction	381
II. Monophyletic origin of Holometabola	382
III. Types of insect larvae	382
IV. Sequence of larval types	389
V. Origin of insect larvae	392
VI. Phylogeny of the orders of Holometabola	396
VII. Types of nymphs and their evolutionary sequence	401
VIII. Summary and conclusions	402
Acknowledgements	403
References	404

INTRODUCTION.

NOTWITHSTANDING the general interest that has been shown in the study of insect transformation, our knowledge of the evolution of larval insects still remains obscure. For the old authorities have followed Brauer (1869) in regarding the diversity of larval forms as being the result of secondary and adaptive modifications of a primitive type; and the modern students, by accepting the theory of Berlese (1913), have recognised that the so-called larvae are but precociously emerged embryos, and that their diversity of types is primarily a consequence of variations in time of emergence. On the one hand, the conception of the adaptive nature of larval insects abases their significance in phylogeny and makes the tracing of their whole evolutionary history unreliable. On the other hand, the ontogenetic sequence of larval types, as illustrated by Berlese, is not conformable to the evolutionary sequence, for the protopod larva is in no way a primitive type. Hence the theories of both Brauer and Berlese, while explaining the significance of the diversity of larval forms in insects, leave the evolutionary side of the problem unsolved.

It is the object of the present paper to deal with this side of the problem of insect transformation that has been so long neglected. The subject will be discussed under its two principal aspects, that is: (1) the larval sequence and (2) the larval evolution properly speaking. By larval sequence we mean the ordered succession of larval types. It is well known that similar types of larvae are often found in very different groups of insects, and that these types usually follow a similar sequence or parallel modifications in the most widely separated orders. But the sequence of larval types is not necessarily phylogenetic, whereas in tracing the larval evolution properly speaking, phylogeny is always involved. In the first case, interest lies in the consideration of the steps by which the various larval types have acquired their characteristic features

in the course of evolution from the most primitive to the most recent. In the second case, it is the origin of insect larvae, of the various orders of Holometabola and their phylogenetic relationships that are to be considered. But in addition it seems desirable to give, first some remarks on the monophyletic origin of the Holometabola, and secondly some account of the different types of nymphs and their evolutionary sequence.

II. MONOPHYLETIC ORIGIN OF HOLOMETABOLA.

In dealing with the problem of larval evolution, the question naturally arises as to whether insect larvae are monophyletic or polyphyletic in origin. In other words, whether the Holometabola have originated from a common ancestor, or whether they have been evolved from several ancestral stocks, arising independently from the Hemimetabola. This old question of insect phylogeny is still unsettled. The monophyletic conception was held by Brauer, Packard (1898) and their followers, since they always claimed the derivation of all existing larval forms from a primitive type. This was chiefly questioned by the palaeontologists, notably Handlirsch (1908), who had traced the holometabolous insects back to several origins in the Hemimetabola. But as we shall see, the evidence obtained from the study of fossil wings is not quite conclusive, and it would be equally possible to deduce the alternative view from the same data. On the other hand, the conception of monophyletic origin of Holometabola, so far as the study of larval forms is concerned, may be justified by the following facts: (1) the development of the wings and other organs of the imago from ingrowing buds is a feature common to all orders of Holometabola. This similarity in the fundamental process of growth indicates similarity of origin. (2) The various types of insect larvae may be successively traced back to a primitive type. (3) The tracing of larval evolution in this sense may help us to explain the phylogenetic relations of the holometabolic orders, and this fact, in its turn, helps to demonstrate the possibility of the single origin of insect larvae. While the first point is clear and needs no remark, the remainder are to be elucidated in the following sections—indeed, the present communication is an exposition of these facts. For the time being, it is only necessary to insist on this monophyletic conception of larval origin in order that it may serve as a basis for further discussions.

III. TYPES OF INSECT LARVAE.

Insect larvae are usually grouped into types either according to their general form (Brauer, Packard), or depending upon their ontogenetic sequence (Berlese). For the purpose of the present study, an attempt is made to characterise the types in a way conformable to their evolutionary sequence, that is, each type is taken to represent a definite advance that has been made in the course of evolution from the most primitive to the most recent; consequently, all the types of side lines are not dealt with.

Following the monophyletic conception of larval origin, the first requisite of such a classification is to distinguish a primitive type versus those derived from it. A comparative study of insect larvae has shown that, among the various groups, the more generalised types usually have better developed appendages, and, as the types become progressively specialised, the appendages are invariably more and more reduced. It seems therefore that the primitive type of larvae would be a type in which all the typical appendages are exhibited in a

well-developed condition¹ and from which the other types have been derived through successive reductions. While the majority of larval types appear to follow this rule, there are, however, some other types the origin of which is undoubtedly different. These latter types are found exclusively among the primary larvae of endoparasitic Hymenoptera; judging from their state of organisation, they are actually in very early stages of morphological development and cannot be considered to have been specialised from other more generalised types. On the other hand, they cannot be regarded as primitive forms, since the parasitic Hymenoptera are by no means primitive Holometabola. The only plausible account of their origin is, therefore, to regard them as representing early stages of ontogenetic development which are ordinarily passed within the egg but which have been, in these instances, brought into the larval state through precocious birth. Hence we may propose to arrange the larval types under three categories, namely, the primitive or generalised type, the specialised types, and the premature types. The primitive type is the type from which all the other types have originated; the specialised types are those which have been derived through modification of pre-existing types, principally by reduction of appendages; and the premature types are those which have owed their existence through precocious emergence from the egg.

1. *The primitive or generalised type.*

The true primitive larva will probably never be discovered, but a living representative is found in the larva of the neuropterous genus *Corydalid* Latreille. This larva, being primitive by its systematic position, exhibits at the same time many generalised features from which the specialised types may be successively traced. It represents, in the sense of Berlese, a typical polypod type; but in the sense of Brauer, a true campodeiform larva, for it resembles *Campodea* Westwood not only in general form but also in structure by being a polypod. We shall designate this primitive type by the term campodeoid-polypod.

The larva (fig. 1) is of large size, massive and robust at its final stage, with a well-developed head, three thoracic and ten distinct abdominal segments. Ten pairs of spiracles are present, including two thoracic and eight abdominal. The antennae are prominent, 4-jointed, and the ocelli are six in number. The mouth-parts resemble those of a Carabid larva, the mandibles are powerful and more or less sharply toothed; the maxillae exhibit the typical parts, with the palpi 4-jointed, the galea palpiform, but the lacinia small, sometimes not well differentiated; the labium consists of a mentum, a broad bi-lobed ligula and 3-jointed palpi. The thoracic legs are well developed, with all the typical parts and paired claws. The abdomen is provided with nine pairs of appendages; each segment except the ninth carries a pair. The appendages consist each of a limb-base or coxite, bearing a large ventral tubercle and a lateral process. The ventral tubercle is called by Snodgrass the vesicle (fig. 1, vs), and the lateral process the stylus (fig. 1, sty). The vesicle is entirely absent on the eighth pair; it is provided with tufts of respiratory filaments on the first seven pairs, but on the last pair, instead of filaments, it is terminated by a pair of claws.

Among the characters which distinguish the present larva as a primitive type, the most important are the abdominal appendages, hence their nature requires consideration. The researches of Heymons (1896) and Snodgrass

¹ It is generally admitted to-day that insects are descendants of polypodous ancestors; hence we may claim the "completeness of appendages" as a feature of prime importance in indicating the "primitiveness of origin."

(1931) have already established the fact that they are rudimentary limbs, but with regard to the homology of their parts, no definite conclusions have yet been reached. Snodgrass considers the limb-base to consist of coxal and subcoxal regions of a typical appendage, the two parts being either distinct or united; the stylus as a rudimentary telopodite; the vesicles as endite lobes of coxae, which in some cases have become normally invaginated. Nevertheless, after admirably discussing the subject, Snodgrass prefers to regard these interpretations as tentative. But if we confine our attention to the mere comparison of living types, and study carefully his work on insect morphology, we can scarcely avoid the conclusion that the abdominal appendicular processes of many insects are respectively homologous structures, that is, between the vesicles of Apterygota, the plantar lobes of caterpillars and sawfly larvae, and the gill tubercles (or vesicles) of *Corydalids* on the one hand; and the styli of Thysanura, the gills of Ephemeroidea larvae, and the lateral processes (or styli) of *Corydalids* and *Sialis* Latreille on the other.

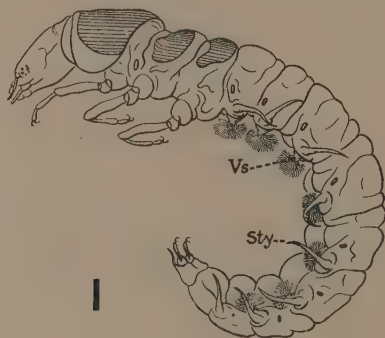


FIG. 1.—Primitive type of larva : campodeoid-polypod larva of *Corydalids*.

The possession by the *Corydalids* larva of abdominal appendages which are homologous with the vesicles and styli of Thysanura affords definite evidence of its primitiveness. This larva may, therefore, be taken to represent the most generalised type of insect larvae from which the other types may have been derived through reductive specialisation. Of course the larva, as a living representative of primitive type, should be very different from the true primitive larva, for it has certainly been much modified in the course of evolution. It would be, however, fruitless at present to trace the actual characteristics of the true primitive larva. But with regard to the abdomen, we may believe, from the known facts of insect morphology, that in the ancestral larva, the typical segmentation, with twelve segments including the telson, might be distinct; the appendages, consisting of the typical parts, might be present on the segments 1-10; the vesicles were probably devoid of respiratory filaments, etc.

2. The specialised types.

The specialised types occur universally in all holometabolous orders. They are extremely diversified in form and structure; but the fact that they have all been derived from the primitive type through successive steps of reductive specialisation has much facilitated the task of their classification. Eight types,

representing the principal steps in their specialisation, are thus recognised and described below.

(1) The Sialoid-polypod type (fig. 2, A). The essential feature of this type is,

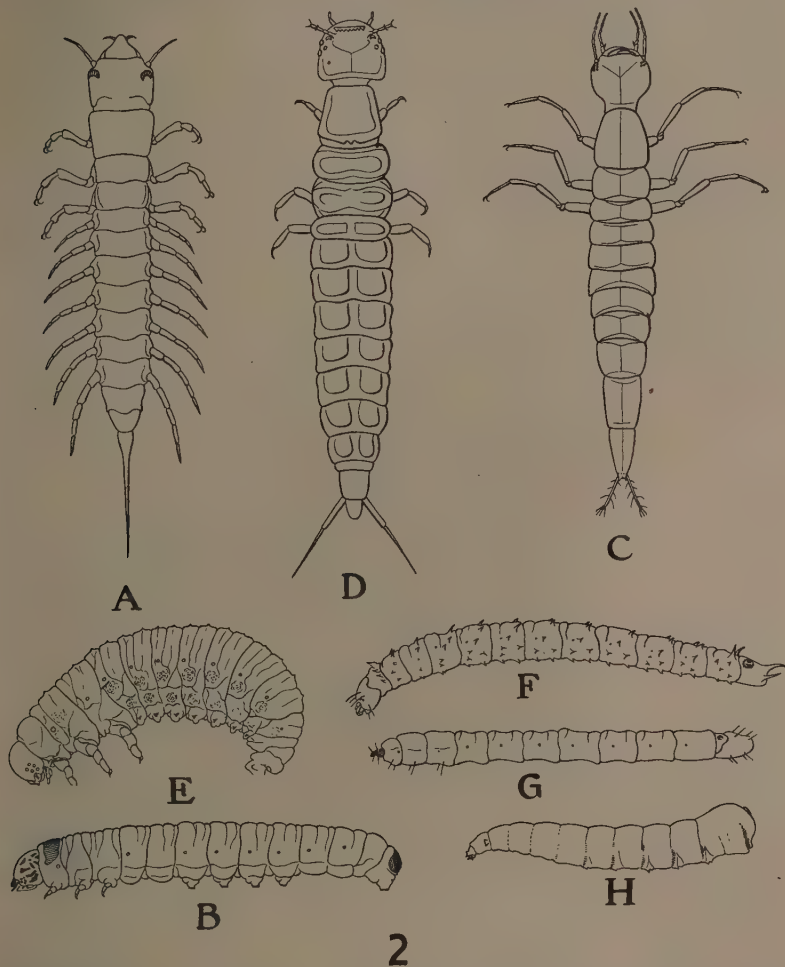


FIG. 2.—Specialised types of larvae: A, sialoid-polypod larva of a Sialid; B, eruciform-polypod larva of an Eucosmid; C, caraboid-oligopod larva of a Dytiscid; D, staphylinoid-oligopod larva of a Staphylinid; E, eruciform-oligopod larva of a Chrysomelid; F, eucephalous-apod larva of a Bibionid; G, hemicephalous-apod larva of an Asilid; H, acephalous-apod larva of a Muscid. Adapted from various sources.

theoretically, the possession of a pair of styli on each of the abdominal segments 1–10, but actually, those of the posterior segments are usually no longer retained. The type seems, therefore, to be derived from the primitive or campodeoid-polypod type by the suppression of vesicles, as such a process also occurs on the

eighth abdominal segment in *Corydalid*. It is found only in certain aquatic larvae, of which the Neuropterons *Sialis* and *Sisyr* Burmeister, the Gyrinid *Dineutes* Aubé, the Dytiscid *Coptotomus* Say, and probably the Hydrophilid *Hydrophilus caraboides* L. (vide Böving and Craighead, 1931), are examples. In *Sialis*, *Sisyr* and *Hydrophilus caraboides*, the styli are evidently present on the seven anterior segments, and in *Coptotomus*, on the six anterior segments; in both cases, each segment carries a pair. But in the Gyrinid, the full number of ten pairs are present; they are distributed on the nine anterior segments, the two terminal pairs being both apparently carried on the ninth segment.

(2) The Eruciform-polypod type (fig. 2, B). Examples of this type are afforded by the larvae of the Lepidoptera, the sawflies, and the scorpion flies. Their essential features are the cylindrical body-shape and the presence of abdominal prolegs. The latter vary much in number, but are primarily of ten pairs, occurring on the segments 1-10. This number is actually found in the sawflies of the family XYELIDAE (Yuasa, 1922), and in the embryonic stage of many Lepidoptera. According to Snodgrass (1931), the typical proleg of a caterpillar consists of three parts, namely, the limb-base or subcoxa, the coxa and the planta; he has brought forward evidence to show that the structure of the planta is almost identical to the vesicle of *Corydalid* larvae. It is therefore the styli of the campodeoid-polypod larvae which are not represented in this type.

(3) The Caraboid-oligopod type (fig. 2, C). The present type is represented by what is ordinarily known as the campodeiform larvae. Among the typical examples are the larvae of most Neuroptera and of many Coleoptera. They resemble those of the campodeoid-polypod and sialoid-polypod types in the flattened-shaped body, the 5-segmented thoracic legs and other characteristics, but have assumed an oligopod condition by the loss of abdominal appendages.

(4) The Staphylinoid-oligopod type (fig. 2, D). The typical representatives of this type are the ordinary campodeiform larvae of the Coleoptera Polyphaga. They can be distinguished from the caraboid-oligopod larvae by their 4-segmented thoracic legs, the tarsal segment being not differentiated. The type is evidently derived from the preceding, since in certain genera of STAPHYLINIDAE (*Philonthus* Stephens, *Bledius* Samouelle), the tarsal segment has still preserved its separated condition, and in *Aleochara bilineata*, it becomes indistinct only from the second instar onwards. The absence of a distinct tarsal segment marks, therefore, an advanced stage in specialisation.

(5) The Eruciform-oligopod type (fig. 2, E). The eruciform-oligopod type is represented by the larvae of several orders, comprising certain sawflies, many Trichoptera, the later stage larvae of the Staphylinid genus *Aleochara* Gravenhorst, one neuropterous family MANTISPIDAE, and the ordinary eruciform larvae of Coleoptera Polyphaga. Although universally characterised by the cylindrical body and absence of abdominal appendages, they are very variable in other respects, and appear to have originated in several ways. In the sawflies, the type is most probably a derivative of the eruciform-polypod type through reduction of abdominal appendages, as the various phases of reduction, from the XYELIDAE and TENTHREDINIDAE to the PAMPHILIDAE, CEPHIDAE and SIRICIDAE are evident. In the Trichoptera, MANTISPIDAE and *Aleochara*, it seems to have been derived from the caraboid-oligopod type by assuming an eruciform shape, for the latter type exists, either in their allied and more primitive families or as primary larvae. Finally, in the Coleoptera Polyphaga, the mode of derivation appears to be similar to that of Trichoptera or Neuroptera, but it is intercalated by a staphylinoid-oligopod type.

(6) The Eucephalous-apod type (fig. 2, F). Eucephalous-apod larvae are characterised by the complete suppression of both thoracic and abdominal appendages but without marked modification in head size and structure. The type occurs in Diptera, in Siphonaptera, in Hymenoptera Apocrita, in certain families of Coleoptera, in the final instars of Strepsiptera and in a few leaf-mining Lepidoptera. In the majority of cases, it appears to have been derived from the oligopod types, more usually the eruciform-oligopod type, through the suppression of thoracic legs. But in Lepidoptera, the apod type follows directly the polypod type without the intercalation of any oligopod forms.

(7) The Hemicephalous-apod type (fig. 2, G). In this type, the head is markedly reduced, usually incomplete posteriorly and becoming more or less retractile into the thorax. The type is characteristic of the Diptera Brachycera, some Nematocera and many parasitic Hymenoptera. It represents the climax of larval specialisation attained by the Hymenoptera, but among the Diptera it is an intermediate type, leading from the more primitive eucephalous type to the much specialised acephalous larvae of Cyclorrhapha.

(8) The Acephalous-apod type (fig. 2, H). This type is the most highly specialised of insect larvae. It is represented by the so-called acephalous larvae of the Diptera Cyclorrhapha in which the head is vestigial, becoming fully and deeply retractile or invaginated within the thorax, and the usual mouth-parts are not developed. The type is evidently derived from the eucephalous type through many intermediate stages.

3. *The precocious types.*

The precocious types are confined to the parasitic Hymenoptera and appear to have been independently acquired by the different groups. Three types, referable to the three earlier embryonic phases of Berlese, are to be recognised, namely, the vermiform-polypod type, the polymerous-protopod type and the oligomerous-protopod type. They all occur in early instars, being invariably followed by a final instar of the usual apod type that is characteristic of all Apocrita. Consequently, they are of more recent origin than the specialised types. It may be said that the Hymenopterous larvae, after attaining their eucephalous or hemicephalous apod state of organisation, have not gone any farther in specialisation than that reached in the Diptera, but new types have been evolved as a result of a shortening in the period of embryonic growth. It is highly improbable that, in the course of evolution, the three types would have developed at the same time; but several steps of premature birth are necessary before a larva can be produced at such an early stage of development as that represented by the oligomerous-protopod type. It is therefore logical to assume that the polypod type is the one that has appeared first, the polymerous-protopod type follows next through further precocious birth, and finally the oligomerous-protopod type which is the one most lately acquired by the Hymenoptera.

Besides these well-marked types, intermediate forms are liable to occur, but our knowledge of the primary larvae of parasitic Hymenoptera is so scanty and imperfect that the true nature of a great many is not yet understood, being masked by superimposed adaptive or secondary modifications.

The cause of premature birth is obscure. While paucity of egg yolk is generally considered as a factor of great importance, it does not seem to be operative in the present instances, since the parasitic embryos are generally enveloped by a trophic membrane which outweighs the deficiency of egg-

yolk. It is therefore not impossible that in these insects precocity of eclosion may be a result of precocious rupture or dissociation of egg envelopes, brought about by the unusual expansion of egg size. Many of the parasitic eggs, after deposition in the host bodies, are found to increase markedly in size until eclosion finally supervenes. Thus in the Ichneumon *Meteorus dimidiatus* Cresson, the newly laid egg measures 0.14 mm. $\times$ 0.04 mm., but it finally attains a maximum size of 1.2 mm. $\times$ 1.5 mm. (Strickland, 1923); in *Dinocampus rutilis* Nees, another Braconid, Jackson (1928) states that the egg may increase in cubic content over 1200 times. The chorion of these parasitic eggs is usually very thin or even membranous, or may be absent, so that it is possible for the egg to absorb, through diffusion or through the action of the inner trophic membrane, the body fluid of the host and to increase enormously its bulk up to the final rupture of the envelopes. If this be the case, then, these

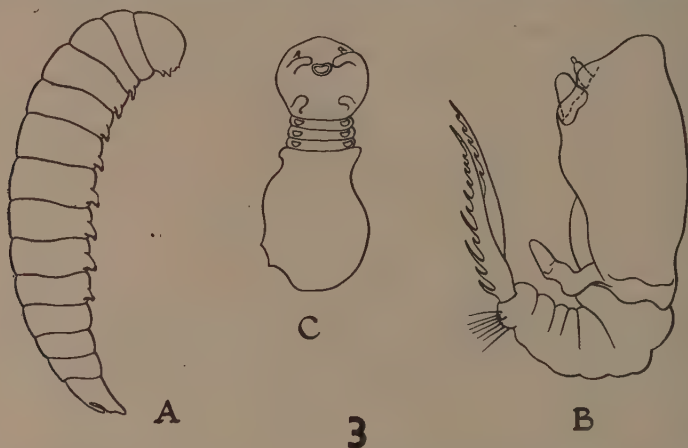


FIG. 3.—Premature types of larvae: A, vermiform-polypod larva of *Phaenoserphus viator*; B, polymerous-protopod larva of *Synopeas rhanis*; C, oligomerous-protopod larva of *Platyaster*. Adapted from different sources.

larval forms would be, primarily, veritable embryos which, after having been brought into the larval state through the precocious rupture of egg envelopes, have survived by reason of their endoparasitic mode of life, and have subsequently acquired superimposed secondary features.

(1) The Vermiform-polypod type (fig. 3, A). The vermiform-polypod type occurs in the Cynipoid families IBALIIDAE (Chrystal, 1930), EUCOILIDAE and FIGITIDAE (James, 1928) and in the Proctotrypid *Phaenoserphus viator* Haliday (Eastham, 1929). Theoretically, it corresponds to Berlese's polypod phase of embryonic development in which the abdomen has just acquired its complete segmentation and full number of appendages. But in actual condition, they are more or less modified, notably in the abdominal appendages which are often subjected to reduction. In *Ibalia* Latreille and *Phaenoserphus* Kieffer, the type is characteristic of the first instar, but in EUCOILIDAE and FIGITIDAE, it occurs in the second instar, while the first observed instar is of the polymerous-protopod type. These two families have attained, therefore, a more advanced stage in their larval evolution.

(2) The Polymerous-protopod type (fig. 3, B). This type is represented by the so-called eucoiliform and cyclopoid larvae of EUKOILIDAE and FIGITIDAE, and probably also by the caudate and teleaform larvae, found in certain genera of Ichneumonoidea, Chalcidoidea and Proctotrypoidea. They are to be compared with Berlese's protopod polymerous stage of embryonic development in which the abdomen has completed its segmentation but does not bear appendages, while the thorax bears rudimentary limbs; but many of them are actually so much modified that their true nature can hardly be recognised.

(3) The Oligomerous-protopod type (fig. 3, C). In this type, the larvae emerge in a very early ontogenetic stage comparable with the protopod oligomerous phase of Berlese; the metamorphosis is still incomplete, the abdomen is not segmented, and the internal organs are not fully differentiated. It is characteristic of certain larvae of PLATYGASTERIDAE, among which the primary larva of *Platygaster herrickii* Packard affords a typical example.

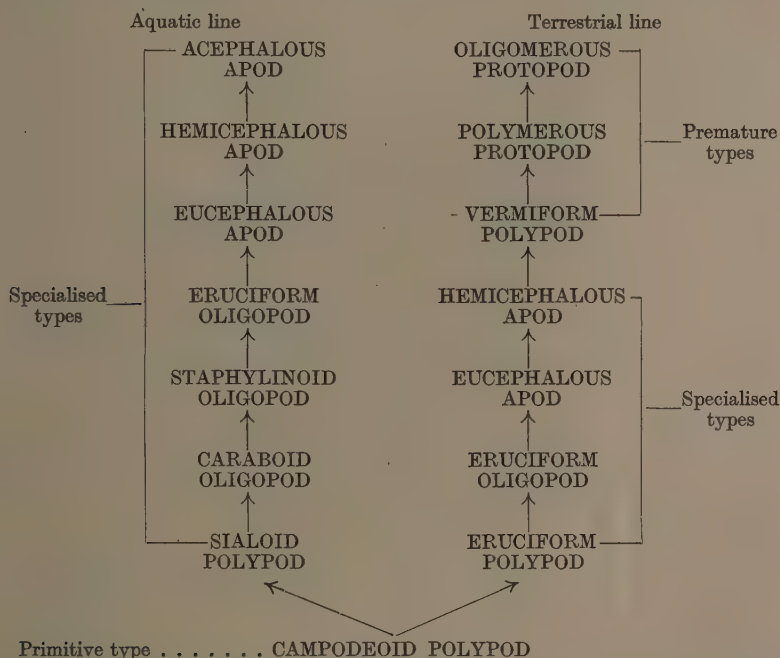


FIG. 4.—Diagram showing the evolutionary sequence of various types of insect larvae.

IV. SEQUENCE OF LARVAL TYPES.

Having characterised the principal types of insect larvae, we may proceed to trace their whole evolutionary sequence; this is illustrated by the accompanying diagram (fig. 4). It is evident that the specialised types, originated from the campodeoid-polypod type, have followed two lines of development: the one, starting from the sialoid-polypod type, culminates in the acephalous-apod type of Diptera; the other, beginning with the eruciform-polypod type, approaches its climax in the hemicephalous-apod type of Hymenoptera which, instead of further specialisation, is followed by the premature types. The first line of

sequence may be designated the aquatic line and the second the terrestrial line. The former comprises the larvae of Neuroptera, Coleoptera, Strepsiptera, Trichoptera, Diptera and Siphonaptera; the latter, those of Mecoptera, Hymenoptera and Lepidoptera. We have seen that all the known sialoid-polypod larvae are aquatic in habit and we have further reasons (to be discussed in later sections) to believe that the orders of this line are primarily aquatic in origin, while those of the second line have been evolved on land. To summarise what has been discussed in the preceding section, the steps of the two lines of evolution are as follows:—

1. Aquatic line. (1) Suppression of abdominal vesicles (sialoid-polypod type) → (2) Complete suppression of abdominal appendages (caraboid-oligopod type) → (3) Disappearance of a distinct tarsal segment on the thoracic legs (staphylinoid-oligopod type) → (4) Assumption of a cylindrical shape of body (eruciform-oligopod type) → (5) Suppression of thoracic legs (eucephalous-apod type) → (6) Reduction and retraction of head within thorax (hemicephalous-apod type) → (7) Further reduction and invagination of head within thorax, atrophy of typical mouth-parts (acephalous-apod type).

2. Terrestrial line. (1) Suppression of abdominal styli, assumption of a cylindrical shape of body (eruciform-polypod type) → (2) Complete suppression of abdominal appendages (eruciform-oligopod type) → (3) Suppression of thoracic legs (eucephalous-apod type) → (4) Reduction and retraction of head within thorax (hemicephalous-apod type) → (5) Moment of eclosion advanced (vermiform-polypod type) → (6) Eclosion further advanced (polymerous-protopod type) → (7) Eclosion still further advanced (oligomerous-protopod type).

The progress of larval specialisation is thus characterised by the progressive reduction of appendages, followed by the reduction and invagination of the head within the thorax combined with the change of body-shape from the flattened to the cylindrical. The most primitive type of insect larvae is, therefore, the type with most completely developed appendages, while the most specialised type has the appendages greatly reduced or completely suppressed. With regard to the premature types, precocity of eclosion being progressively brought about, the less developed protopod types follow the more highly developed polypod types in their evolutionary sequence.

The evolutionary history of the sawfly larvae may be taken as a partial illustration of the sequence. In this group of insects, the succession of several types of larvae is traceable from the typical eruciform-polypod type, through various phases of reduction, to the oligopod and apod types. The hypermetamorphosis of the *MELOIDÆ* affords another example in which the first instar is of the staphylinoid-oligopod type, but the second instar assumes an eruciform-oligopod type which may be followed by a final instar of apod type. But if the sequence is generally followed by insects of different orders, it is also subjected to curtailment. For instance, the apod larvae of Lepidoptera appear to have been directly derived from the eruciform-polypod type without the intercalation of the transitional eruciform-oligopod type. In the Diptera, the apodous larvae, before attaining their actual condition, might have passed through several transitional oligopod and polypod phases, but owing to the possibility of abbreviations in evolution, their exact history is unknown. On the other hand, in the hypermetamorphosis of the Hymenoptera, the ontogenetic sequence is exactly the reverse of the evolutionary sequence, but this is conceivable from their mode of origin.

On the whole, the evolution of larval types, starting from a common ancestral form, has followed two lines of sequence and two modes of origin. While this conclusion is justifiable from what has been discussed above, its significance requires further elucidation.

In the first place, we perceive from the above study that a similar sequence of larval evolution towards reductive specialisation is followed in general by the most widely different orders of Holometabola irrespective of their origin and habits. The sequence appears thus to represent a definite trend of evolution. If we compare this remarkable trend towards reductive specialisation, or more especially the sequence of appendage-suppression with that of appendage-development in the embryo, certain correlations may become apparent. In the embryo, the development of appendages proceeds, as a general rule, from the anterior backwards. The rudiments of antennae usually appear first; they are followed by those of mouth-parts, of thoracic legs and finally by those of abdominal appendages (*vide* Dawydoff, 1928). Now, in the evolution of larval types, the reduction, or more especially the suppression, of appendages goes on precisely in the opposite direction; it is the abdominal appendages which disappear first, the thoracic legs, mouth-parts and antennae following successively. It seems therefore that the reductive trend of larval evolution follows a general rule, that is, the later an organ is differentiated in the embryonic stage, the more it is susceptible to reduction or suppression in the larval stage. Furthermore, the trend continues to go on in the embryogeny: as the larva is progressively specialised, the time of inhibition becomes more and more advanced. Thus in *Donacia* Fabricius, all abdominal appendages except the first pair are suppressed from the embryogeny; and in the Diptera, all body-appendages are no longer existent in the embryonic stage. In short, the sequence of larval types appears to be governed by a definite trend towards reduction of appendages, which in its turn is determined by the sequence of development of these appendages in the embryo.

Secondly, in following the definite trend of evolution, it will be found that larvae, while being progressively specialised, invariably become more and more differentiated in structure from the adult. Thus larval growth may be said to represent a deviation of morphogenesis from the original line of development, while larval evolution is characterised by leading that deviation to become more and more accentuated. Consequently, the more specialised types of larvae have to undergo greater changes in their transformation to the adult stage. But the most important feature of holometabolism is without doubt the retardation or inhibition in the growth of adult organs. This inhibition of growth, being progressive, is generally less extended in the primitive forms but gradually amplified in the specialised types. Moreover, the progression in the extent of inhibited growth is always accompanied by an increase in amount of change during metamorphosis. Hence we may conclude that the evolution of insect larvae through increasing deviation of morphogenesis is primarily determined by the tendency towards increasing retardation or inhibition of imaginal growth, of which the progressive reduction of appendages is but an outward expression.

Thirdly, it is evident from the foregoing discussions that the specialised types of larvae are not to be regarded as representing recapitulations of ancestral embryonic phases, for the assumption of a given larval type in a given insect is determined by the nature of its previously existing type of larva, or more fundamentally by the degree of imaginal inhibition attained by that insect. Moreover, in the course of evolution, there is actually a tendency towards

progressive retardation in time of eclosion. We have come to this conclusion because: (1) in animal development, increasing complexity in evolution is generally accompanied by corresponding prolongation in embryonic growth; and (2) the existence of two or more types of larvae in certain cases of hypermetamorphosis (for instance in MELOIDÆ) is a proof that in normal metamorphosis, the identity of the more primitive type of larva, in being modified to give rise to a new form, has habitually come to be passed in the egg stage and thus retarded the time of birth. The specialised types of larvae present, therefore, characters rather contrasting to the premature types. For we have seen that in the latter case, the larvae are primarily embryos and their sequence of evolution is followed by a progressive advancement in time of eclosion instead of their being retarded.

Thus the evolution of larval types is manifested by the following definite trends: the trend towards progressive reduction of appendages which is governed by the trend towards increasing inhibition of imaginal growth, and among the premature types, the trend towards progressive shortening in the period of embryonic growth.

Arriving at this point of our discussion, we may return to the introductory remark to see how the theories of Brauer and Berlese can be reconciled with the present view in regard to the significance of the diversity of larval types. Brauer's theory appears sound in considering all insect larvae to have been derived from a common ancestor; but the adaptability of larvae as a principal factor of evolution claimed by him is only of secondary importance. Berlese's theory explains well the origin of the premature types but fails to account for the specialised types which, by their universal occurrence in all orders, must be considered as the most important of larval forms.

V. ORIGIN OF INSECT LARVAE.

The origin of insect larvae presents a problem of great interest, since it signifies the origin of the Holometabola or of holometabolism in insects. At the same time, several points for inquiry arise: Firstly the mode of origin, that is how, in the course of evolution, the immature Hemimetabola in the form of one nymph has been transformed into the differentiated larva and pupa of Holometabola. Secondly the milieu of origin: that is, in what habitat did the primitive larvae develop? Thirdly the time of origin: that is, in what epoch of geological history did the first Holometabola appear? All these points are to be dealt with in the present section.

1. *Mode of origin.*

It is almost universally admitted that the Pterygota are the descendants of Apterygota, and the Endopterygota (or Holometabola) the descendants of Exopterygota (or Hemimetabola). As insects are the only winged Arthropods, they must, at some period in the history of their development, have passed from an originally wingless to a winged condition; and among the earliest winged insects so far discovered, the most generalised Palaeodictyoptera are evidently hemimetabolous. But the difficulty arises in explaining how the transition from the nymph of Hemimetabola to the differentiated larva and pupa has been brought about.

In dealing with the problem, it is necessary to consider at first the nature of the ancestral nymphs. The most primitive of existing nymphs are found in the order Ephemeroptera. In this order, the nymphs exhibit many features

which are undoubtedly of very primitive nature; thus the possession of a generalised type of mouth-parts with crustacean mandibles and well-developed superlinguae, the presence of a pair of long cerci and a median caudal filament on the eleventh abdominal segment and the retention of abdominal styli in the form of gills are all characters highly suggestive of those of Thysanura. But the Ephemerid nymphs, though primitive, are certainly already specialised; for instance, the abdominal vesicles which are characteristic of both Thysanura and primitive forms of larvae are notably absent. It appears therefore that the earliest nymphs, being ancestral to larvae and themselves derived from forms resembling existing Thysanura, should likewise possess abdominal appendages consisting of styli and vesicles. Hence we may visualise the primordial nymphs as forms belonging similarly to the campodeoid-polypod type, but differing from the primitive larvae in the possession of compound eyes, median ocelli, well-developed antennae, long cerci and median caudal filament besides the external wing rudiments.

These considerations show that there was, originally, a general conformity in body-form and abdominal structure among the three great divisions of the class Insecta. Consequently it appears that the larvae do not represent any earlier stage of morphological development than that reached by the nymphs as the theory of Berlese maintains; and that they would have been simply derived from the latter through the reduction of visual organs, antennae and caudal appendages—or in other words, through degeneration and parasitism, as many authors believe. It may be noted, however, that the absence of compound eyes and well-developed antennae in larvae may well be the result of progenesis or precocious birth. In the early instars or primary nymphs of may-flies, which (as we shall see later) are evidently hatched at a very early stage of development, the compound eyes are represented by ocelli-like structures and the antennae are rudimentary. Moreover, in certain Hemimetabola (ALEYRODIDAE and COCCIDAE) in which a tendency towards holometabolism is clearly manifested, the young also emerge at an earlier stage than usual.

Nevertheless, the most important difference between the nymphs and larvae lies neither in the presence or absence of certain structural characters, nor in the stage of development they represent, but in the mode of development. In the typical nymphs of Hemimetabola as well as in the early stage nymphs of Ephemeroptera, growth is apparently directed towards gradual completion of imaginal features. In the larvae, many of the adult characters are more or less held in an embryonic state in the form of undifferentiated imaginal germs, and growth apparently proceeds in a different way; it leads to the pupal stage. The differentiation of immature Holometabola into the double forms of larva and pupa is, therefore, essentially a result of inhibition in the growth of adult characters in the larval stages. The origin of this inhibition of imaginal growth is obscure, but it must be sought for in the egg. It is interesting to note that the Palaeozoic holometabola were usually of much smaller size than the Hemimetabola of the same era, consequently it appears that they may have developed from much smaller eggs. The Palaeodictyoptera are generally recognised as the probable ancestors of Holometabola, and these primitive forms were very large insects; their wing-length normally ranges from 45 to 75 mm., rarely below 30 mm., and sometimes reaching the gigantic size of 160–190 mm. as in the genera *Megaptilus* Brongniart and *Homoeophlebia* Handlirsch (*vide* Handlirsch, 1908). On the other hand, the wings of Palaeozoic Holometabola attain only a length of about 10 mm. It is therefore

possible that the sudden shortening of egg-size or egg-provisions may play an important rôle in determining the inhibition of imaginal growth. If this view were correct, we may figure the origin of holometabolism as follows: "In the course of evolution of the class Insecta, a Palaeozoic Hemimetabola, by certain genetic changes, has produced eggs which contain an unusually small amount of food reserves; the eggs eventually developed, giving rise to the first insect larva in which growth of some of the lately appeared characters was more or less inhibited and held undifferentiated in the form of imaginal germs." Thus the larval instar arises as a consequence of inhibition in imaginal growth which is primarily determined in the egg, and which leads to a deviation of morphogenesis from the original line of development. The pupal instar arises as a consequence of imaginal inhibition in the larval stage—it restores the original line of development of the insect by escaping from the inhibitory control.

2. *Milieu of origin.*

The problem of the original milieu of insect larvae has been notably dealt with by Lameere (1899), who maintained that "l'holométabolisme est dû à la pénétration de l'insecte à l'intérieur des tissus végétaux." Consequently, according to Lameere, the oldest larvae must have had a burrowing or mining habit. But according to the foregoing studies on the larval sequence, we are led to adopt a quite different view that "insect larvae appear to have been originally aquatic in habit rather than phyto-parasitic or terrestrial." For not only the most generalised type of existing larvae are without exception aquatic, but many of the principal orders as well show evidence of aquatic origin.

In tracing the evolution of larval types, we have shown that the various types of insect larvae, being derived from a common ancestral form, have followed two ecological lines of sequence, one terrestrial and the other aquatic. The ancestral or primitive forms, actually exemplified by the campodeoid-polypod larvae of the neuropterous family CORYDALIDAE, are all aquatic in habit. Of the derived types, while some have acquired a terrestrial habit and have been differentiated into the orders Mecoptera, Hymenoptera and Lepidoptera, others have been retained in the aquatic medium and have diverged in the course of evolution into the orders Neuroptera, Coleoptera, Trichoptera and Diptera. Thus in Neuroptera, all larvae belonging to the two most primitive families, CORYDALIDAE and SIALIDAE, are found in water; in Coleoptera, out of the ten families included in the more primitive suborder Adephaga, five are exclusively aquatic; in Trichoptera, the early stages are almost without exception passed in water; in Diptera, the majority of the Nematoceros families are either entirely or pre-eminently aquatic in their larval stage. On the other hand, aquatic adaptation is always a rare and exceptional phenomenon in the orders of the terrestrial line, and whenever it occurs is invariably confined to the more specialised forms. As to the two other orders of the aquatic line, the Strepsiptera and Siphonaptera, their want of aquatic representatives is to be explained by their being secondary in origin.

It may be opposed, however, that in the Coleoptera and Diptera, the terrestrial larvae of such families as CARABIDAE and BIBIONIDAE are to be considered as forms of more generalised structure and hence of more primitive origin than the aquatic larvae of their respective allied families. But in these particular cases, generalisation of structure is not necessarily correlated with primitiveness of origin. For insects as a whole are primarily terrestrial; if the

primitive larvae were proved to be aquatic in habit (the existing facts are in favour of this view), it only means that the first Holometabola have arisen in a condition in which their larval stage was adapted to be passed in water. In other words, if insect larvae originated in the aquatic milieu, the terrestrial forms are to be regarded as having re-acquired the original habit of the class. At the early stages of their evolutionary history, the primitive aquatic larvae would not present much adaptive modification, whence the terrestrial forms arose and have retained a somewhat more generalised type of structure; whereas the aquatic forms might be further modified in adaptation to their habitat and exhibit physiognomy of a somewhat more specialised nature. The terrestrial forms thus derived were liable to be re-adapted to life in water, consequently the aquatic larvae are likewise of two different origins, including those which are primarily aquatic and those which are secondarily aquatic. By following these considerations, we can understand why the overwhelming majority of aquatic larvae are found in families of more primitive nature, and why these larvae, while belonging to more generalised types in evolutionary sequence, usually exhibit a much higher degree of adaptive modification than the secondary aquatic larvae, of similar habit, found in the more specialised families.

Besides the general reasons given above, we may examine more specially the two cases in question. In the case of Coleoptera, it is noteworthy that the sialoid-polypod larvae, while representing the most primitive type of the order, are without exception aquatic. They are found in the families GYRINIDAE, DYTISCIDAE and HYDROPHILIDAE. With respect to the latter family, it is also of interest to note that the larvae of the two subfamilies LIMNEBINAE and HYDRAENINAE are even considered by Böving and Craighead (1931) to be of more primitive nature than those of the Adephaga. The development of the two suborders Adephaga and Polyphaga, as we shall presently see, must have taken place at a very early stage in the evolution of the Coleoptera. Consequently, it is conceivable that there should be a great number of aquatic forms present in the more primitive families of Polyphaga; whereas in the higher groups (Heteromera, Phytophaga, Rhynchophora and Lamellicornia), there are but few such cases found in the families CHRYSOMELIDAE and CURCULIONIDAE; these latter forms are evidently secondary in origin. In the case of Diptera, while the Bibionid larvae are structurally very primitive, their adult forms present evidence of specialisation in the reduction of wing veins and in the assumption of holoptic eyes in the males. And, if we were to accept the amphipneustic and metapneustic conditions of respiration as features of aquatic adaptation, we might regard the whole suborder of Cyclorrhapha as having originated from those aquatic forms which have been already specialised.

In short, all the above facts seem to support the view that insect larvae were primarily aquatic in habit, and the transition from the hemimetabolous to the holometabolous type of development, which is essentially characterised by a changing mode of morphogenesis, has taken place in the aquatic milieu.

3. Time of origin.

The Holometabola appear to be a very ancient group. The existence among their larval forms of a campodeoid-polypod type resembling so much the generalised Thysanura indicates that the group probably made its first appearance at a comparatively short time after the appearance of the Hemimetabola. This conception is wholly in accord with the palaeontological data, since in the Lower Permian times, authentic Holometabola were already abundant. The

studies of Tillyard (1926, 1932) have shown that in the Lower Permian Beds of Kansas, U.S.A., not only the Mecoptera were rich in varieties and species, but the three suborders of Neuroptera, the Sialoidea, Raphidioidea and Planipennia, were represented by distinct and comparatively highly specialised types. It seems therefore that the earliest Holometabola must have developed not later than Upper Carboniferous times.

But the study of Tillyard (1926) has gone still further; he was able to show that the small Upper Carboniferous wing of *Metropator pusillus*, placed by Handlirsch in the order Palaeodictyoptera, is a true Mecopteron and, consequently, a true Holometabola. With regard to its mecopterous affinity, we shall have something to say in the following section in discussing the phylogeny of the Holometabola, but the small size and the venational features of the wing leave little doubt as to its holometabolic nature. Hence we have to look back for the origin of Holometabola to a more remote period in geological history. Now, the age of *Metropator* Handlirsch is of Lower Upper Carboniferous, and, seeing that fossilisation can only preserve an infinitely small part of the fauna or flora of a given period, while of those preserved, only an infinitely small part are available for study, we may safely conclude that at this age, the Holometabola must have already attained a certain degree of development, and consequently they must have originated at a time not later than the Lower Carboniferous.

VI. PHYLOGENY OF THE ORDERS OF HOLOMETABOLA.

In this section, we shall see how the views advanced in the foregoing pages may help us to explain the origin and phylogeny of the various orders of Holometabola. To do this, we have to appeal also to other domains of entomology among which palaeo-entomology stands first in importance as being possible to afford direct evidence. Fortunately, recent studies in fossil insects have brought to light a certain amount of data which may enable us to get some rough idea of the evolution of the Holometabola. The subject will, accordingly, be dealt with under the three following headings: (1) the nature of the primitive Holometabola, (2) the principal lines of holometabolous evolution and (3) the origin of the orders.

1. Nature of the primitive Holometabola.

We have seen that the Holometabola made their first appearance possibly in the Lower Carboniferous period, but their earliest manifestations are unknown. The most primitive of Holometabola so far recorded is *Metropator pusillus* from the Upper Carboniferous, and this is the only insect of holometabolous type known from that period. It is therefore of great interest to see what is the nature of this Carboniferous Holometabola and, together with that of the Lower Permian forms, how it may permit us to draw certain conclusions about the characteristics of the ancestral Holometabola.

The nature of the *Metropator* wing (fig. 5) is liable to be disputed. While it is regarded by Tillyard as a true Mecopteron, its affinity to Neuroptera is none the less obvious, as the long subcosta and the broad costal space are both neuropterous features. The subject, however, may be better approached by considering at first the relative antiquity of the two orders in question. The Mecoptera are generally believed to represent the oldest order of Holometabola from which the majority of the other orders are capable of derivation. The abundance of these insects in the Lower Permian times and their venational

affinities with the early types of many holometabolous orders are probably the reasons for this belief. But from many points of view, the order Neuroptera must be considered as the most primitive of all existing Holometabola, and consequently older than the Mecoptera. For ontogenetically, the Neuroptera present a larval type which is theoretically the most closely related to the primitive larvae; while the mecopterous larvae represent evidently a more specialised type. Ecologically, the neuropterous larvae are primitively aquatic, a habit conforming in speculation to that of the earliest Holometabola, but those of Mecoptera appear to have been evolved on land. Palaeontologically, while the Mecoptera were abundant in the Lower Permian period, the fact that the Neuroptera were represented at the same period by very specialised types indicates an even more ancient origin. These considerations, supported by the venational features noted above, may well lead us to believe that *Metropator pusillus* is more closely allied to Neuroptera than to Mecoptera.

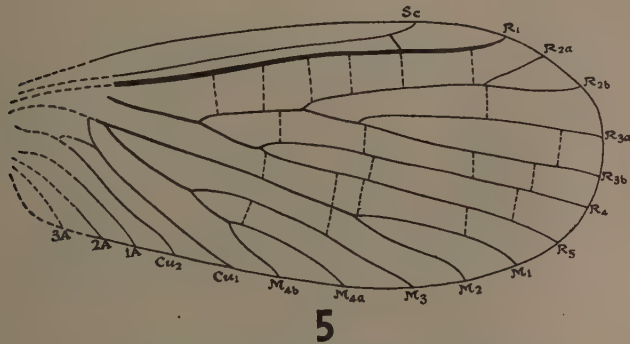


FIG. 5.—Wing of *Metropator pusillus*. After Tillyard.

But if the Neuroptera were proved to be the most primitive of living Holometabola and *Metropator pusillus* to be a Neuropteroid, we cannot yet conclude that the earliest Holometabola were of the Neuropteroid type. As Holometabola would have had a very remote origin, there should exist a long series of transitional forms leading from the earliest types to the Neuroptera. Moreover, the primitive forms of Coleoptera, or Protocoleoptera, being very different from the Neuroptera in venational features, are not to be regarded as having arisen from Neuropteroid ancestors. It is noteworthy, however, that with the exception of Coleoptera, all the main orders of Holometabola are referable to neuropterous ancestry (to be presently discussed); we may thus draw a preliminary conclusion that the ancestral form of Holometabola has given rise, in the course of evolution, to the early types of both Neuroptera and Coleoptera. Now the early types of both orders are characterised by a long subcosta and a broad costal space, and, as these features are also common to the Protorthoptera, we must assume that the earliest Holometabola are the forms which exhibit certain relationships with the Protorthoptera. But the latter as a group are already more or less specialised, hence to account for the origin of the Holometabola, the most agreeable hypothesis is that "the Holometabola appear to have originated from a Palaedictyopteroid stock (or even a still earlier stock) which is more or less allied to, and probably contemporary with, that giving rise to Protorthoptera."

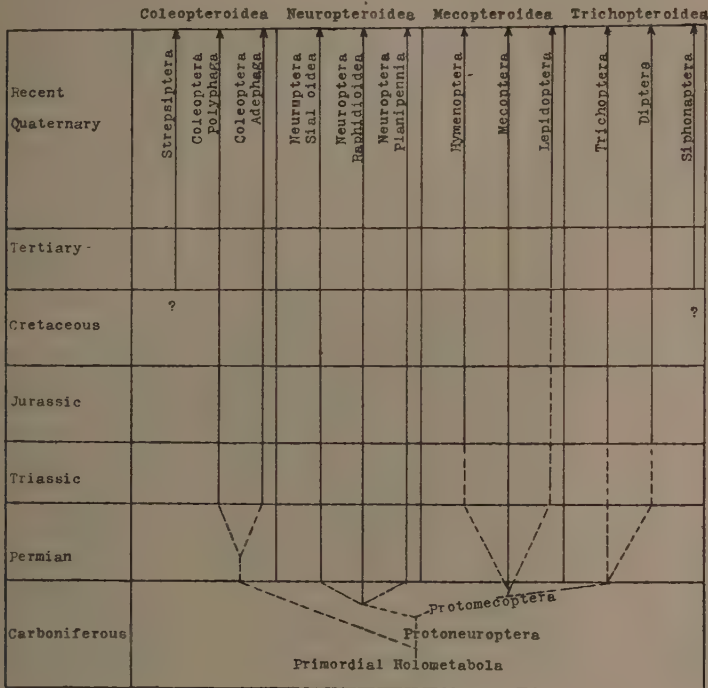
2. Principal lines of evolution.

The earliest Holometabola are thus to be presumed as forms which exhibit certain relationships with the Protorthoptera, their larvae are probably aquatic in habit and possess a complete set of body appendages. From these early forms might have arisen the ancestral forms of Protocoleoptera as well as those of Neuroptera. The formation of these two primary lines of evolution must have taken place at a very early period, since the Neuroptera were proved of great antiquity and the ancestors of the Coleoptera, before attaining the form of Protocoleoptera with tegminous elytra would, originally, have membranous fore-wings. The ancestral forms of true Neuroptera, though not discovered, may be conveniently designated as the Protoneuroptera. The Protoneuroptera have probably given rise to two groups of insects, the Neuroptera and the Protomecoptera. The community of descent of these two groups is clearly manifested by the venational features of such forms as *Choristosialis enigmatica* (Tillyard, 1932) and *Protomerope permiana* (Tillyard, 1926). The Protomecoptera, in turn, appear to have given rise to the groups of Mecopteroidea and Trichopteroidea, as the venational affinities of their early forms tend to indicate. It seems therefore that the PROTOMEROPIDAE and some of the other mecopterous forms discovered in the Lower Permian beds are not true Mecoptera, since their larvae should be of a more generalised type and aquatic in habit in order that, from them, both the aquatic Trichopteroidea and terrestrial Mecopteroidea might have originated. In other words, Protomecoptera and their derivatives, the true Mecoptera, must have co-existed in the Lower Permian and Pre-Permian times. Thus in their early history, the Holometabola have probably followed four principal lines of evolution: namely, the Coleopteroidea, the Neuropteroidea, the Mecopteroidea and the Trichopteroidea (fig. 6). The Coleopteroid line represents an early offshoot and comprises actually the orders Coleoptera and Strepsiptera; the Neuropteroid line comprises the single order Neuroptera; the Mecopteroid line the orders Mecoptera, Hymenoptera and Lepidoptera; the Trichopteroid line the orders Trichoptera, Diptera and Siphonaptera.

3. Origin of the orders.

(1) The Coleopteroid orders. The Coleopteroid line of evolution is chiefly directed to the development of the order Coleoptera. Although true Coleoptera elytra are not known until the Triassic period, and the earliest fossils which may be recognised as generalised Coleopteroid types are not known until the Upper Permian age, the order appears to have had a more remote origin. For in Triassic rocks, fossil elytra were abundant, including already specialised types, some of which have been referred to the families CHRYSOMELIDAE and CURCULIONIDAE. We are thus led to believe that the tegminous remains of the Upper Permian are not the immediate ancestors of existing Coleoptera, but are to be regarded as specialised branches of the very ancient group Protocoleoptera which have extended to that period; and that true Coleoptera must have developed from the still earlier progenitors not later than or even before the Permian age. The Protocoleoptera of the Upper Permian are nevertheless of such great significance that they permit the following presumption with regard to the evolution of the Coleoptera. Firstly, the nature of these fossil wings tends to indicate that the Coleoptera, before the fore-wings had attained their present condition of structure, passed through a series of transitional stages in which these organs were tegminous and with clearly marked veins

like those of many Hemiptera. This conclusion is quite in agreement with the view put forward above, that the Coleopteroid line represents an early offshoot of holometabolous evolution. Secondly, since some of the fossils, namely, the PERMOPHILIDAE, present notable resemblance to the existing HYDROPHILIDAE, we can at least suppose that the larvae and even certain adults of these ancient forms were aquatic in habit, and that the two suborders Adephaga and Polyphaga must have developed at a very early stage in the evolutionary history of the order. These propositions, as we have seen, are also conformable to the facts presented by living Coleoptera.



6

FIG. 6.—Geological distribution and probable relations of the orders of Holometabola.

The origin of the order Strepsiptera appears most obscure. While the assumption of a staphylinoid-oligopod type by their primary larvae may indicate certain relationship with the Coleoptera Polyphaga, they are so different in other respects as to render improbable the belief that they are directly derived from the latter. It is possible that they might have arisen from a common stock with the Coleoptera, but without further evidence all speculations on the subject are fruitless.

(2) The Neuropteroid order. The Neuropteroid line of evolution is represented by a single order Neuroptera, which is the most primitive of all living orders of Holometabola. These insects have certainly existed in the Upper Carboniferous or even at a time earlier than that. Their ancestral forms,

together with those of Coleoptera, are probably the earliest branches of Holometabola. They have retained many primitive features in the subcostal venation of wing, the form of prothorax, the structure of larvae, etc. It appears certain that the order has never given rise to any other groups except the three which already existed in the Lower Permian, namely, the Sialoidea, the Raphidioidea and the Planipennia.

(3) The Mecopteroid orders. The Mecopteroid orders here concerned are the Mecoptera, the Hymenoptera and the Lepidoptera; but in a broad sense, Trichopteroidea should also be included.

The most generalised types of Mecopteroidea so far known are the Protomecoptera of the Lower Permian times. The venation of these early forms, with its profuse ramifications and widened costal space, is so closely allied to that of Neuroptera that the two groups most probably have arisen from a common stem, the theoretical Protoneuroptera. The Protomecoptera are further characterised by the development of Macrotrichia on the wing (observed by Tillyard, 1926) and by the retention of aquatic habit in the larval stage (discussed above). Both these points are of great significance, since they afford a basis from which the evolutionary tendencies of the Mecopteroid orders (*sens. lat.*) may be traced. It appears certain that all these orders are derivable from the Protomecoptera, yet their inter-relationships are obscure, more especially with regard to the Hymenoptera, of which no direct evidence is available. Now, on the basis of these two important characters, it is possible to show that the orders in question have followed two lines of evolution, the one (Mecopteroidea *sens. str.*) characterised by the reduction of wing trichia and the re-acquisition of terrestrial habits in the larval stage, the other (Trichopteroidea) by the increasing development of wing trichia and the retention of original larval habits. Consequently the Hymenoptera, by the conformation of wing structure, larval type and habit, must be regarded as being closely allied to the true Mecoptera in origin, like the Diptera to the Trichoptera.

But the position of the order Lepidoptera becomes problematical, since it agrees, on the one hand, with the Trichoptera and Diptera in the development of wing trichia, and, on the other hand, with the Mecoptera and Hymenoptera in the re-acquisition of terrestrial habit by the larvae. The close affinity of the Lepidoptera and Trichoptera has long been recognised, and the development of wing trichia in both orders tends also to support the view. But the change of habit in the larval stage, accompanied by the loss of abdominal styli and the assumption of a uniform eruciform-polypod type, are characters common to all the three orders Mecoptera, Hymenoptera and Lepidoptera; and this conformity of characters must be considered to indicate community of descent. We have thus grouped the three orders together to represent a terrestrial line of evolution in contrast with the Trichopteroid orders which represent an aquatic line, both arising from the Protomecoptera.

The true Mecoptera must have had a very remote origin, since they were abundantly represented, and co-existed with the Protomecoptera, in the Lower Permian times. The earliest known Hymenoptera occur in Upper Jurassic strata and those of Lepidoptera in rocks of Eocene age, but it is practically certain that both orders have appeared on the earth at a respectively earlier period. Although true Lepidoptera are of more recent origin than true Hymenoptera, yet on account of their affinity with the Trichoptera, their ancestral forms would appear to have become detached from the main stem of Mecopteroid evolution at an earlier period than those of the Hymenoptera.

(4) The Trichopteroid orders. Included in this series are the orders

Trichoptera, Diptera and Siphonaptera. The origin of the Siphonaptera is very obscure; they are generally considered to be related to the Diptera because their larval characters resemble those of certain Nematocera. On the other hand, the community of descent of the Trichoptera and Diptera is manifested in many ways, notably in the similarity of larval habit and of development of wing trichia as discussed above, and in the venational affinities of their possible ancestral forms (Paramecoptera, Paratrachoptera and Protodiptera) as observed by Tillyard (1937). The two first-mentioned features, while characterising almost all the living Trichoptera, have been retained only in some of the more primitive groups of modern Diptera. As to the venational affinities of the three extinct groups, Tillyard's conclusions appear to be indubitable; but owing to the difference of larval habits, these groups cannot be regarded as having been derived from the true Mecoptera as he believed. The Paramecoptera, probably descended from the Protomecoptera, might be taken as the fore-runners of Trichoptera; similarly the Protodiptera, evidently related to the Paratrachoptera, exhibit features ancestral to the Diptera. But between these extinct groups of the Permian times and the two modern orders the earliest fossils of which were recorded in the Jurassic rocks, no annectant forms have yet been discovered.

VII. TYPES OF NYMPHS AND THEIR EVOLUTIONARY SEQUENCE.

It seems appropriate to add here a brief discussion on the evolution of the nymphal forms. Nymphs, like the larvae of Holometabola, are referable to a number of types and have followed a similar sequence in evolution, although they have not attained such a diversity of form and structure as that found in the larvae. The following principal types may be recognised.

(1) The Campodeoid-polypod type. This is presumably the most primitive type of nymph. It is no longer existent among the living groups of Hemi-metabola; but from the reasons previously stated, we must believe that such a type did exist and was characteristic of the earliest forms. Nymphs of the present type were certainly more primitive in organisation than the primitive larvae; as we have seen, they would have very generalised mouth-parts, ten pairs of typical appendages on the first ten abdominal segments, a pair of long cerci and a median caudal filament on the eleventh segment, long antennae, well-developed compound eyes and three ocelli. They were literally Thysanura carrying wing-rudiments. The intercalation of a nymphal stage in insect development may be thus explained as the result of a progressive evolution in organisation (*i.e.* the acquisition of wings) without the corresponding prolongation in embryonic growth.

(2) The Ephemeroid-polypod type. This type is characteristic of the nymphs of Ephemeroptera. It is found also among Plecopteroid insects in the existing family EUSTHENIIDAE and in the Permian order Protoperlaria (Carpenter, 1935). The type is evidently derived from the preceding by the suppression of abdominal vesicles. It is therefore comparable with the sialoid-polypod type of larvae and represents a parallel stage of evolution.

(3) The Blattoid-oligopod type. By far the great majority of existing nymphs are referable to this type which is derived from the Ephemeroid-polypod type through further suppression of abdominal styli. The type parallels the caraboid-oligopod type of larva in stage of evolution and, according to Berlese, represents a post-oligopod phase of development.

Besides these principal types which are characterised by the progressive

suppression of abdominal appendages, there are others following different modes of evolution. For instance, the primary nymphs of may-flies evidently originated by way of progenesis. For these nymphs always issue from the egg at a stage in which the abdominal gills are not yet developed, the mouth-parts are still rudimentary, the antennae are only represented by a few segments, the compound eyes are mere ocelli-like structures and the internal systems are still incompletely differentiated (*vide* Lestage in Rousseau, 1921). They are comparable with the polymerous-protopod phase of embryogeny, although they are well advanced in organisation in certain respects, such as the development of thoracic legs. In the Thysanoptera, ALEYRODIDAE and COCCIDAE, the tendency towards inhibition of imaginal growth in early nymphal instars is clearly manifested so that the insects leave the egg not as ordinary nymphs but as incipient larvae which are finally followed by an incipient pupal stage.

There is thus a close parallelism in evolutionary tendencies between the nymphs of Hemimetabola and the larvae of Holometabola. Moreover, the differentiation of the post-embryonic period of growth into larval and pupal stages so characteristic of the Holometabola occurs also in some groups of Hemimetabola.

Finally, we may summarise here the various ways by which the different nymphal and larval forms were originated. These ways are: (1) by further complications in evolution without corresponding prolongation in embryonic growth, (2) by progenesis or shortening in period of embryonic growth, (3) by inhibition in imaginal growth and (4) by reductive specialisation; but in all cases, the evolution of a given form is often complicated by caenogenesis. The first-mentioned factor or process of evolution is of common occurrence in the animal kingdom and is especially characteristic of the lower groups of Metazoa such as Porifera and Coelenterata. It accounts for the origin of nymphs or of metamorphosis in insects, since the Apterygota are generally regarded as ametabolous. The existence of more than two types of larvae in the life history of many hypermetabolous insects (MELOIDAE, MANTISPIDAE, etc.) is of similar origin. The second factor accounts for the origin of the primary larvae of many endoparasitic Hymenoptera and of the primary nymphs of Ephemeroptera. The third factor explains the origin of larvae or of holometabolism in insects as well as the origin of incipient larval instars in certain Hemimetabola. Lastly, the fourth factor, that of reductive specialisation, is the most characteristic feature of the evolution of the larval and nymphal types.²

VIII. SUMMARY AND CONCLUSIONS.

In this paper, the author has discussed some aspects of the problem of larval evolution in insects and has arrived at the following conclusions.

1. All insect larvae are derivable from a common ancestor.
2. The primitive larvae are presumably of the campodeoid-polypod type, having three pairs of thoracic and ten pairs of abdominal legs; the latter bear each a vesicle and a stylus.
3. From the primitive type, the various types of existing larvae appear to

² The various examples of hypermetamorphosis may be roughly classified under two types according to their mode of origin: (1) The meloid type, comprising the typical examples of hypermetamorphosis found in the Coleoptera, Strepsiptera, Neuroptera and Diptera, originated through the retention of more archaic type or types of larvae in the early instars; or, in other words, through the specialisation of the later stage larvae without corresponding prolongation in embryonic growth. (2) The figitid type, characteristic of many parasitic Hymenoptera, originated through the progenesis of embryonic forms.

have been derived in two ways : by specialisation and by progenesis. Those of former origin are designated as specialised types ; those of latter, as premature types.

4. Specialisation of larval types has taken place chiefly through the reduction of appendages which proceeds from the posterior part of the body to the anterior. The progress in reductive specialisation is governed by the progress in degree of inhibition in imaginal growth. Consequently, the evolution of the specialised larval types follows a sequence proceeding from the polypod state to the apod, and the assumption of a given type by any given insect depends, primarily, upon the degree of imaginal inhibition attained by that insect.

5. Progenesis of larval forms has been brought about probably by the precocious rupture of egg envelopes. The evolution of premature types follows a sequence which is the inverse of the embryonic sequence in normal insect development ; the assumption of a given type of premature larvae by any given insect depends, primarily, upon the stage in organisation in which eclosion takes place.

6. The larva arises as a consequence of inhibition in imaginal growth which is initiated in the egg and which leads to a deviation of morphogenesis from the original line of development. The pupa arises as a consequence of imaginal inhibition in the larval stage ; it restores the original line of development of the insect concerned by escaping from the inhibitive control.

7. The earliest larvae were probably aquatic in habit ; they appear to have developed at a time not later than the Lower Carboniferous and from a Palaeodictyopteroid stock, more or less allied to that giving rise to the Protorthoptera.

8. From the primordial Holometabola might have arisen the ancestral forms of the Protocoleoptera as well as those of the Protoneuroptera, representing the two earliest lines of holometabolous evolution. The Protoneuroptera gave rise to the early types of Neuroptera and Protomecoptera ; the Protomecoptera to Mecopteroidea and Trichopteroidea ; the former comprises the orders Mecoptera, Hymenoptera and Lepidoptera, the latter the orders Trichoptera, Diptera and Siphonaptera.

9. The nymphs of Hemimetabola, like the larvae of Holometabola, are referable to a number of types and exhibit similar tendencies in evolution. The primordial nymph was theoretically campodeiform and polypodous, resembling exactly a generalised Thysanuran carrying wing-rudiments and differing from the primitive larval forms in the possession of compound eyes, median ocelli, well-developed antennae and long caudal appendages as well as in the wing-rudiments.

ACKNOWLEDGEMENTS.

The author is greatly indebted to Dr. A. D. Imms, F.R.S., who, through the friendly recommendation of Dr. L. E. R. Picken of the Sino-British Science Co-operation Office, has kindly consented to read the manuscript and take charge of its publication. The author is also indebted to Mr. B. Young for assistance in preparing the illustrations.

REFERENCES.

- BERLESE, A., 1913, Intorno alle metamorfosi degli insetti. *Redia* 9 : 121-38.
- BÖVING, A. G., and CRAIGHEAD, F. C., 1931, *Larvae of Coleoptera*. Brooklyn.
- BRAUER, F., 1869, Betrachtung ueber die Verwandlung der Insekten in Sinne der Descendenz-Theorie. *Verh. zool.-bot. Ges. Wien.* 19 : 299-318.
- CARPENTER, F. M., 1935, The Lower Permian Insects of Kansas. Part 7. The Order Proterperlia. *Proc. Amer. Acad. Arts Sci.* 70 : 101-46.
- CARPENTER, G. H., 1921, *Insect Transformation*. London.
- CHRYSTAL, R. N., 1930, *Oxf. For. Mem.* 11.
- DAWYDOFF, C., 1928, *Traité d'Embryologie comparée des Invertébrés*. Paris.
- EASTHAM, L. E. S., 1929, The post-embryonic Development of *Phaenoserphus viator* Hal. *Parasitology* 21 : 1-21.
- HANDLIRSCH, A., 1908, *Die Fossilen Insekten*. Leipzig.
- HEYMONS, R., 1896, Über die abdominalen Körperanhänge der Insekten. *Biol. Zbl.* 16 : 855-64.
- IMMS, A. D., 1937, *Recent Advances in Entomology*. London.
- , 1938, *A General Textbook of Entomology*. London.
- , 1942, *Outlines of Entomology*. London.
- JACKSON, D. J., 1928, The Biology of *Dinocampus (Perilitus) rutilus* Nees. *Proc. zool. Soc. Lond.* 1928 : 597-630.
- JAMES, H. C., 1928, On the life-histories and economic status of certain Cynipid parasites of Dipterous larvae. *Ann. appl. Biol.* 15 : 287-316.
- LAMEERE, A., 1899, Discours sur la raison d'être des métamorphoses chez les Insectes. *Ann. Soc. ent. Belg.* 43 : 619-36.
- LESTAGE, J. A., 1921, in Rousseau, *Larves et Nymphes aquatiques des Insectes d'Europe*. Bruxelles.
- PACKARD, A. S., 1898, *A Textbook of Entomology*. New York.
- SHARP, D., 1895, Insects. *Camb. Nat. Hist.* 5.
- SNODGRASS, R. E., 1931, Morphology of the Insect Abdomen. *Smithson. misc. Coll.* 85, No. 6.
- STRICKLAND, E. H., 1923, *Bull. Agric. Can. (N.S.)* 26.
- TILLYARD, R. J., 1926, Kansas Permian Insects. Part 7. The order Mecoptera. *Amer. J. Sci.* 11 : 133-64.
- , 1932, Kansas Permian Insects. Part 14. The order Neuroptera. *Amer. J. Sci.* 23 : 1-30.
- , 1937, The ancestors of the Diptera. *Nature* 139 : 66-7.
- YUASA, H., 1922, A Classification of the Larvae of the Tenthredinoidea. *Illinois biol. Monog.* 7, No. 4.

E x D

Vol. 97. Part 16. Pp. 405-418, 6 figs.

20th November, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation : Trans. R. ent. Soc. Lond.

CONTENTS

	PAGE
X Tsai, P. H., and TANG, C. The classification of the Chinese gall Aphids with descriptions of three new genera and six new species from Meitan, Kweichow	405-418, 6 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 4s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.	} <i>Vice-Presidents</i> .
C. B. WILLIAMS, M.A., D.Sc.	
H. B. WILLIAMS, LL.D.	

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.
J. W. EVANS, M.A., D.Sc.
G. FOX-WILSON, N.D.H.
R. M. GREENSLADE.
FRANCIS HEMMING, C.M.G., C.B.E.
H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.
MISS C. E. LONGFIELD.
SIR GUY A. K. MARSHALL, K.C.M.G.,
D.Sc., F.R.S.
G. E. J. NIXON, B.A.
J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.
FRANCIS HEMMING, C.M.G., C.B.E.
H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.
O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.
B. M. HOBBY, M.A., D.Phil.
J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.
W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.
K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.
N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.
E. A. COCKAYNE, M.A., M.D., F.R.C.P.
CAPT. R. A. JACKSON, R.N.
COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.
THE HON. MIRIAM ROTHSCHILD.
W. H. THORPE, M.A., Sc.D.
N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

- 1. British National Committee for Biology** (Royal Society).
Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.
Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.
- 2. Local Committee of Management of Wicken Fen.**
Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].
- 3. National Trust for Places of Historic Interest or Natural Beauty.**
Mr. H. M. Edelsten, O.B.E., appointed 1944.
- 4. New Forest Association.**
Mr. W. Fassnidge, appointed 1934.
- 5. New Forest Joint Committee.**
Mr. W. Fassnidge, appointed 1939. *Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.*
- 6. Royal Meteorological Society. Phenological Committee.**
Dr. C. B. Williams, M.A., D.Sc., appointed 1937.
- 7. Biology War Committee.**
Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.
- 8. Council for the Promotion of Field Studies.**
Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.
- 9. Joint Bioclimatic Committee.**
Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

THE CLASSIFICATION OF THE CHINESE GALL APHIDS WITH DESCRIPTIONS OF THREE NEW GENERA AND SIX NEW SPECIES FROM MEITAN, KWEICHOW

By P. H. TSAI and C. TANG.

(Department of Entomology and Plant Pathology, National University of Chekiang.)

(Communicated by the Honorary Secretary.)

Manuscript received 27th March, 1946.

(Read 2nd October, 1946.)

WITH SIX TEXT-FIGURES.

A TOTAL of nine species of Chinese gall-nut Aphids living on Sumac were studied, of which six are new to science and one is new to the fauna of China. The material reported in this paper was collected from the neighbourhood of Meitan, Kweichow, by the authors and their colleague during 1942-43.

The nine species found in Meitan may be separated by the following key.

Key to genera and species of Chinese gall-nut APHIDIDAE.

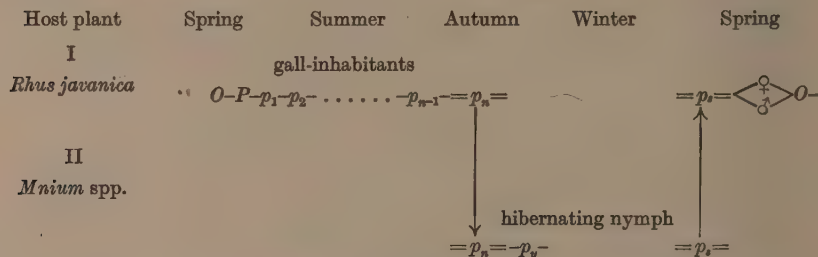
(Subfamily ERIOSOMATINAE, Tribe Fordini.)

- 1 (6). Antennae of alate form 5-jointed (galls on *Rhus javanica*; exits located at the apex of the gall).
- 2 (3). Stigma of fore-wings elongated, sickle-shaped, the 3rd antennal joint of alate form, at least in the case of spring migrants, the longest, sensoria without fringed setae *Melaphis*¹ Walsh.
- 2A. 3rd antennal joint of the fall migrant longest, much longer than the 5th, the boundaries of sensoria well defined, gall angulated
Melaphis chinensis Bell.
- 2B. 3rd antennal joint of the fall migrant a little shorter than the 5th, the boundaries of sensoria somewhat obsolete, gall egg-shaped
Melaphis peitan sp. n.
- 3 (2). Stigma much shorter, truncated at the distal end
Nurudea Matsumura. (4)
- 4 (5). Apical 2 joints of the antennae without complete annulation
Nurudea subgenus *Nurudea*.
- 4A. The apical 2 joints of the antennae each with a very large ovoid sensorium, occupying nearly $\frac{4}{5}$ surface of the joint
Nurudea (*Nurudea*) *sinica* sp. n.
- 5 (4). Apical 2 joints of the antennae with annulation, sensoria sometimes with conspicuous fringed setae
Nurudea subgenus *Nurudeopsis* Matsumura.
- 5A. Ring-shaped sensoria broader, the distribution on the joints III : IV : V = 4 : 3 : 5; galls not prominently reddish, with the surface densely pubescent *Nurudea* (*Nurudeopsis*) *shiraii* Matsumura.
- 5B. Ring-shaped sensoria narrower, the distribution on the joints III : IV : V = 11 : 7 : 9; galls rosy red (new to China).
Nurudea (*Nurudeopsis*) *rosea* Matsumura.

¹ Except some individuals of an American species, *Melaphis rhois*, which has 5- or 6-jointed antennae.

- 6 (1). Antennae of alate form 6-jointed (galls on *Rhus punjabensis* var. *sinica*, exits located at the base of the gall).
- 7 (8). Stigma of fore-wings elongated, sickle-shaped, the apical 2 antennal joints the longest, sensoria fringed with setae
- Meitanaphis** gen. n. (**Meitanaphis elongallis** sp. n.).
- 8 (7). Stigma not sickle-shaped.
- 9 (10). Each joint of antennae with a large oblong sensorium, fringed with inconspicuous setae
- Macrorhinarium** gen. n.
- 9A. Antennae and wings shorter; galls egg-shaped
- Macrorhinarium ovogallis** sp. n.
- 9B. Antennae and wings longer and slender; gall ensiform with a curved hook at its apex **Macrorhinarium ensigallis** sp. n.
- 10 (9). Each joint of antennae with several annulated sensoria, fringed with setae **Floraphis** gen. n.
- 10A. Galls irregularly branched from the base, rosy red
- Floraphis meitanensis** sp. n.

The life-history of *Melaphis peitan* in Meitan is summarised in the following scheme :—



O , eggs; $-P$ -, stem mother or fundatrix; $-p_1- \dots -p_n-$, wingless viviparous female generations on the primary host or fundatrigeniae; $=p_n=$, winged viviparous female in autumn or fall migrant; $-p_v-$, newly hatched young; winter point for the hibernating nymph; $=p_s=$, winged viviparous female in spring or spring migrant or sexupara; $\varnothing\delta$, sexuals; from newly hatched young to the spring migrant may also be described as virginogeniae which live in general on the secondary host.

Melaphis peitan sp. n. (fig. 1).

Full migrant (winged viviparous female) : antennae 5-jointed, shorter than the head and thorax combined, the 5th joint longest, the 3rd longer than the 4th. Joint I subcylindric, armed with a few bristle-like hairs; II globular also with a few tubercled bristles; III and remaining joints cylindric, except the third joint tapering proximad, which is inserted in a cup-shaped depression of II. Each joint from III to V is armed with a number of irregular oval sensoria, somewhat branched in form, which vary greatly in number, as the boundaries of sensoria are somewhat obsolete and contemporaneous with the formation of the sclerotised islands; the actual number of sensoria cannot be counted. Joint V, like those upon the other joints, is armed with many sensoria upon the whole (dorsal and ventral) surface of the postrhinial. Anterhinial very short, imbricated, the length subequal to its width, only $\frac{1}{4}$ the length and of a half-breadth of the postrhinial, at the apex with 4 short hairs.

Head castaneous brown in colour; front greenish-black; vertex dark brown, straight

or slightly depressed near the median line. Eyes black, with the ocular tubercles distinct. Ocelli 3, dark brown, present in their normal position. Antennae light fulvous with the proximal two joints castaneous. Rostrum pale grey, black distad, extends near to the middle coxae.

Prothorax dusky green, pterothorax castaneous brown, the alinotum is darker than the sterna. Fore-wing transparent, slightly marked with imbrications; venation normal; stigma of the fore-wing is greyish-green, darker at its hind margin, sickle-like in form, extending to the apex; near the middle part of the fore-wing there are 7-8 circular sensoria placed between the Sc and R. The radial sector (stigmatic nervure) is long and slightly curved, at the proximal end relatively broad and conspicuous. Media simple, short, only $\frac{2}{3}$ the length of the stigmatic nervure, at the basal half obsolete. The cubitus and the first anal vein are straight, separated at their base. Veins fulvous in colour. The hind-wing

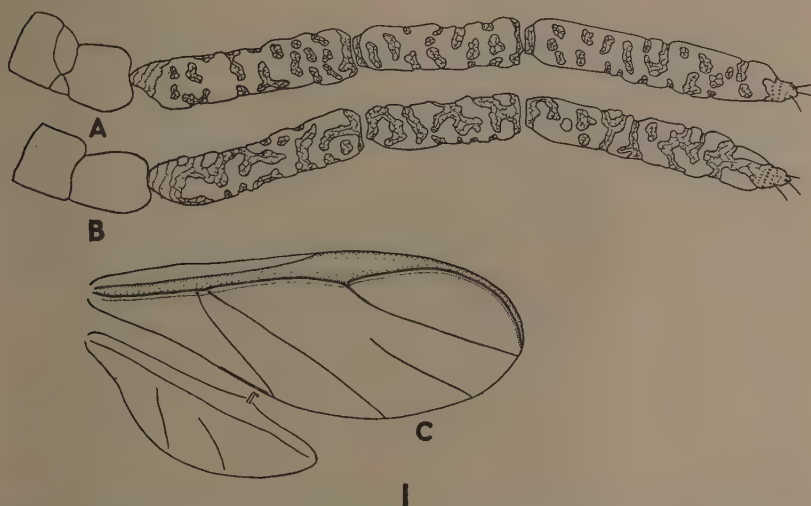


FIG. 1.—*Melaphis peitan* sp. n. (Fall migrant). A. antenna (ventral view); B. antenna (dorsal view); C. wings.

also hyaline, radial sector, media and cubitus almost straight, the latter widely separated from the media. Both media and cubitus (the 2 obliques) are obsolete for some distance at their bases. Two (sometimes 3) fine, overcurving, bristle-like hooklets at the costa, and the hind margin of the fore-wing thickened to receive them. Axillaries of wing light green. Legs moderately long; tibiae less stout than the antennae, with many short setae; fore and middle tibiae subequal, hind ones longer; tarsi marked with imbrications.

Abdomen greenish-black, twice the length of the thorax. The body colour of mounted specimen in balsam (treated in turpentine only), yellow; eyes reddish-black; ocelli reddish-purple. Legs and antennae fulvous, stigma and veins are pale fulvous.

Measurements: length of body 1.52 mm.; width of head (across eyes) 0.34-0.38 mm.; antenna 0.51 mm. (I, 0.032 mm.; II, 0.045 mm.; III, 0.139 mm.; IV, 0.109 mm.; V, 0.186 mm.); length of fore-wing 2.1 mm.; hind leg: femur and trochanter, 0.301 mm.; tibia, 0.482 mm.; tarsus, 0.120 mm.

Nymph of the fall migrant: antennae 5-jointed. At the distal end of postrhinarial with a fringed primary rhinarium, but that of IV joint sometimes inconspicuous. Head greyish-green; eyes variable from dusky green to black; ocelli from dusky green to red. The

colour of specimen mounted in balsam (treated with turpentine only): eyes reddish-black, ocelli red. Rostrum short, chro-leucus, not reaching the 2nd coxae, with the distal part black; antennae translucent, milky chro-leucus. Prothorax and abdomen greenish, pterothorax yellow, legs and wing pads also milky chro-leucus.

Measurements: length of body 1.36 mm.; antenna 0.50 mm. (relative length: I, 19; II, 19; III, 48; IV, 39; V, 67); hind leg: femur and trochanter, 0.241 mm.; tibia, 0.258 mm.; tarsus, 0.086 mm.

Newly hatched young (laid by fall migrant): body pale green, oblong; antennae much stouter, 4-jointed; and 4th joint the longest, its anterhinial short; the 3rd and 4th joints each with a primary rhinarium which is fringed with conspicuous setae, and on the 3rd is small and circular, on the fourth is large, oblong, and transverse in position. Eyes reddish-purple, composed of three facets; rostrum long, far beyond the 3rd coxae, with small black pattern at its distal part.

Measurements: length of body 0.291 mm.; width 0.157 mm.; antenna 0.113 mm. (relative length: I, 8; II, 8; III, 9; IV, 16); hind leg: femur and trochanter, 0.051 mm.; tibia, 0.051 mm.; tarsus, 0.028 mm.

Spring migrant (Sexupara) (winged viviparous female). In coloration it is hard to distinguish the spring migrant from the fall migrant, but the relative lengths of the joints of the antennae are different in the two forms. Inasmuch as the 3rd joint of the spring migrant is the longest joint, yet shorter in comparison with the 5th joint of the fall form, it therefore unquestionably still belongs to the genus *Melaphis*. The 4th is less than half the length of the 5th, and the 5th subequal to the 3rd. The sensoria are apparently demarcated, oval, oblong or rhomboid in form, and the distribution on each joint is as follows: III-50; IV-18; V-45. Wings marked with imbrications, the prolongation of the stigma much shorter than that of the fall migrant. The prolongation of the 2nd oblique of the hind-wing meets with the 1st oblique near the base. Hooklets 2 or 3.

Measurements (one specimen only): length of body 1.2 mm.; antenna 0.43 mm. (relative length: III, 11.5; IV, 5; V, 10.5); hind leg: femur and trochanter, 0.379 mm.; tibia, 0.499 mm.; tarsus, 0.103 mm.

Male: body dusky green, oblong. Waxy covering delicate, white, downy. Vertex rounded. Antennae 4-jointed; the 4th joint the longest, the rest subequal. Anterhinial distinct, the length subequal to its width, with 4 short hairs at the apex. Rostrum absent, but the remnants of the trophic tubercle present. Tibiae stouter than the antennae.

Measurements: length of body 0.445 mm.; width 0.191 mm.; antenna 0.114 mm. (IV, 0.076 mm.); hind leg: femur and trochanter, 0.065 mm.; tibia, 0.085 mm.; tarsus, 0.017 mm.

Oviparous female: body yellowish-brown, oval. Waxy covering about the same as that of the male. Vertex straighter than that of the male. Antennae 3-jointed. Functional mouth-parts wanting. Tibiae stouter than the antennae. After 3rd moulting, a large solitary egg appears in the abdomen.

Measurements: length of body 0.508 mm.; width 0.254 mm.; antenna 0.090 mm. (I, 0.014 mm.; II, 0.0197 mm.; III, 0.0563 mm.); hind leg: femur and trochanter, 0.070 mm.; tibia, 0.085 mm.; tarsus, 0.017 mm.

Fundatrigeniae (wingless viviparous females): body turmeric yellow, antennae 5-jointed. Distal part of the 4th joint and of the postrhinial, each with a fringed primary rhinarium. Rostrum long, extending far beyond the 3rd coxae, black distad.

Measurements: length of body 0.696 mm.; width 0.565-0.696 mm.; antenna 0.268 mm. (relative length: I, 12; II, 13; III, 14; IV, 17; V, 36); hind leg: femur and trochanter, 0.189 mm.; tibia, 0.155 mm.; tarsus, 0.069 mm.

Galls: galls greenish-yellow in colour, with soft short hairs, very large, some of them measuring about 62 by 40 mm., and of an egg-like form, hence the name *peitan*. Sometimes the surface is more or less roughened by protrusions, with a large cross-like slit on top

of these protrusions, later split open, resembling the petals of a flower, from which the winged fall migrants emerge.

Syntype: slide specimens collected by the authors in 1942 are preserved in the Entomology Laboratory, College of Agriculture, National University of Chekiang.

Habitat: Meitan (Kweichow).

Host: Primary host, *Rhus javanica* Thunb.; galls produced on leaflets.

Secondary host: hibernating nymph on moss (*Mnium* sp.).

Nurudea (*Nurudea*) sinica sp. n. (fig. 2).

Fall migrant (winged viviparous female): antennae 5-jointed, shorter than the combined length of head and thorax; the 3rd joint being the longest, nearly twice the length of the

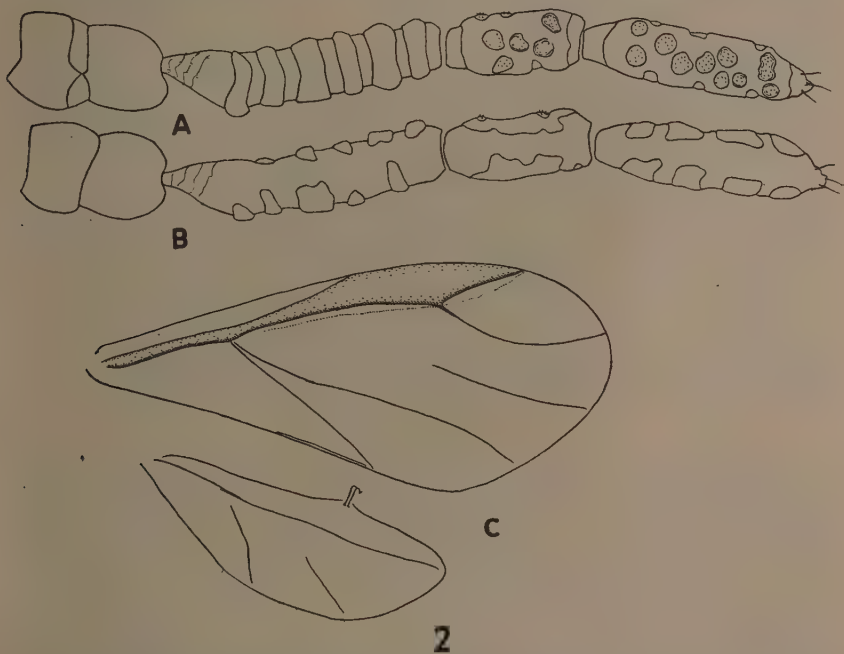


FIG. 2.—*Nurudea* (*Nurudea*) *sinica* sp. n. (Fall migrant). A. antenna (ventral view); B. antenna (dorsal view); C. wings.

4th, 5th longer than the 4th but shorter than the 3rd. The 3rd is marked with about 7-8 complete annulations, the 4th and 5th without distinct annulations, but each with a large sensorium enveloping nearly $\frac{1}{2}$ the surface of the joint; the median rib with rudimentary projections, sometimes with one developed ring on the proximal end of IV and one to two rings on V; the rest could be traced by their obsolete sclerotised islands, which usually are oval or subcircular in shape, scattered over more than half the surface of each sensorium. Anterhinarial very short, with 3 short hairs at the apex, the length less than its width, only $\frac{1}{10}$ the length and nearly as broad as the postrhinarial at the base.

Head castaneous brown in colour. Eyes purplish-black, with distinct ocular tubercles;

ocelli 3 in number, blackish, present in their normal positions. Antennae pale fulvous. Rostrum pale fulvous, and extends to between the 1st and 2nd coxae;

Prothorax pale yellowish-green or yellowish-brown, pterothorax castaneous brown. Fore-wings transparent; venation normal, stigma of fore-wing greyish-green or grey, darker at its hind margin, oblique in form. The radial sector curved, proximal end broader and conspicuous, media simple, at the basal half obsolete. The 2 obliques separated at the base, the 2nd one downward near the outer margin. Veins pale fulvous in colour. The hind-wing also hyaline; radial sector almost straight; both media and cubitus curved and obsolete for some distance at their bases; 2 hooklets on the costa. Axillaries of wing light green. Legs moderately long, tibiae less stout than the antennae, with many short setae; fore- and mid-tibiae subequal, the hind one longer.

Abdomen pale yellowish-green or yellowish-brown.

Measurements: length of body 1.03 mm.; width of head (across eyes) 0.24–0.26 mm.; antenna 0.41 mm. (I, 0.031 mm.; II, 0.042 mm.; III, 0.142 mm.; IV, 0.072 mm.; V, 0.102 mm.); length of fore-wing 1.72 mm.; hind leg: femur and trochanter, 0.293 mm.; tibia, 0.396 mm.; tarsus, 0.103 mm.

Galls: pale yellowish-brown, the surface exposed to direct sunlight is light pinkish colour; shape somewhat irregular in form, some being fusiform, with few large globose protuberances on the apex, with a slender short stalk proximally. The largest gall measured about $55 \times 40 \times 30$ mm., the smallest one $45 \times 19 \times 15$ mm. only. Exits made on the apex of the protuberances.

Syntype: slide specimens collected by the authors in 1942 are preserved in the Entomology Laboratory, College of Agriculture, National University of Chekiang.

Habitat: Meitan (Kweichow).

Host: primary host, *Rhus javanica* Thunb. Galls situated on the wings of the leaves.

This species is closely allied to the Japanese *N. ibofushi* Matsumura, but differs in the structure of sensoria on apical two joints of the antennae.

Meitanaphis gen. n.

Antennae shorter than the head and thorax combined, 6-jointed, the 3rd and 4th joints short, subequal in length, the 5th and 6th joints long, also subequal, the 5th or 6th joint longer than the 3rd and 4th combined, antehinarial short; each joint with a very large prominently fringed sensorium, which occupies $\frac{2}{3}$ the surface of the joint, on each sensorium are scattered many oval or island-shaped setigerous plates. Head nearly rectangular, the anterior margin straight, broader than the length; ocular tubercle present; ocelli very large, situated in normal position; rostrum short, reaching somewhat beyond the 2nd coxae. Fore-wing ample, the first 2 obliques not united at the base; media simple, at the basal half obsolete; stigma very long, sickle-shaped, extending far before the apex. Hind-wing with both media and cubitus present, with 2 hooklets at the costa. Cornicles wanting; cauda small and round; legs slender and moderately long.

Apterous form with 5-jointed antennae and 3-facet eyes; the antennae of new larva 4-jointed.

Genotype: *Meitanaphis elongallis* sp. n.

This resembles *Melaphis* Walsh, but differs from it in the number and proportion of antennal joints, and in the curious form of the sensoria.

Meitanaphis elongallis sp. n. (fig. 3).

Fall migrant (winged viviparous female): body dusky green, oblong; antennae 6-jointed, shorter than the head and thorax combined, the 1st and 2nd joints globular, the 2nd joint more or less longer than the 1st, the 3rd and 4th joints very short, subequal in length, the 5th and 6th joints much longer and subequal in length, usually with the 5th a little shorter than the 6th. The flagellar joints evenly with a large fringed sensorium occupying more than $\frac{2}{3}$ of the whole surface. On the sensorium are scattered many oval or island-shaped plates which bear the fringed and median setae. The number of sclerotised islands on the sensoria of each joint varies with the order and the individuals. The average number of islands is as follows: III, 13 (9–20); IV, 12 (4–19); V, 50 (42–69); VI, 43 (35–53). Anterhinaria short, the length subequal to its width, only $\frac{1}{3}$ the length and $\frac{3}{4}$ the breadth of the postrhinarial, at the apex with 4 short hairs.

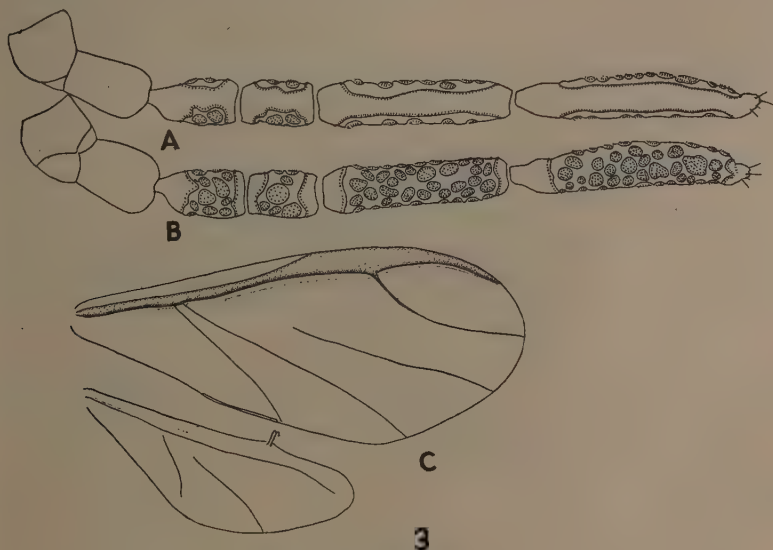


FIG. 3.—*Meitanaphis elongallis* sp. n. (Fall migrant). A. antenna (dorsal view); B. antenna (ventral view); C. wings.

Head fuscous in colour; vertex straight. Eye purplish-black, the ocular tubercles distinct; ocelli pale yellow, 3 in number, present in their usual positions. Antennae pale greyish-brown. Rostrum pale green, extending to midway between the pterothorax.

Pterothorax fuscous. Wing shining and hyaline, more slightly marked with imbrications. Stigma of the fore-wing dusky green, sickle-like, extending far before the apex; all veins greenish-brown; stigmatic nervure stout, black proximally; media simple, weak, a little longer than the stigmatic nervure, obsolete in the basal third; the cubitus and 1st anal vein separate at their bases, the former slightly curved downward; radial sector of hind-wing curves at the apex forking incidentally; media and cubitus weak, separated at base. Hooklets 2 in number (sometimes only 1). Axillaries of wings dusky green. Legs moderately long; tibiae less stout than the antennae, with many short setae; fore and middle tibiae subequal, hind one longer.

Abdomen dusky green, twice the length of the thorax.

Measurements: length of body 1.3 mm.; width of head (across eyes) 0.32–0.36 mm.; antenna 0.52 mm. (I, 0.038 mm.; II, 0.049 mm.; III, 0.065 mm.; IV, 0.058 mm.; V, 0.130 mm.; VI, 0.155 mm.); length of fore-wing 2.0 mm.; hind leg: femur and trochanter, 0.310 mm.; tibia, 0.396 mm.; tarsus, 0.103 mm.

Fundatrigeniae (apterous viviparous females): body fuscous to turmeric, oval in form. Antennae pale fulvous, almost translucent, short, 5-jointed. At the distal part of the 4th joint and of the postrhinial each with a small fringed round primary rhinarium. Eye purplish-black, composed of 3 facets. Rostrum pale fulvous, black distad, extends near to the 3rd coxae. The colour of legs is similar to that of antennae. Tibiae a little stouter than the latter.

Measurements: length of body 0.8 mm.; width 0.57 mm.; antenna 0.26 mm. (relative length: I, 10; II, 14; III, 11; IV, 16; V, 34); hind leg: femur and trochanter, 0.173 mm.; tibia, 0.114 mm.; tarsus, 0.062 mm.

Newly hatched young (found in gall): body oblong, while alive pale yellowish-green in colour. Eye black. After mounting in balsam (treated in turpentine only) body yellow, eye red, composed of 3 facets. Antennae 4-jointed, the 2nd, 3rd and 4th joints each gradually increasing in length. There is a small round fringed primary rhinarium distally on the 3rd joint and a large oblong one transversely on the distal end of postrhinial. Rostrum black distad, extending far beyond the 3rd coxae.

Measurements: length of body 0.413 mm.; antenna 0.163 mm. (relative length: I, 8; II, 10; III, 16; IV, 23); hind leg: femur and trochanter, 0.104 mm.; tibia, 0.085 mm.; tarsus, 0.042 mm.

Galls: small, green in colour, elliptical, distal end stouter than the proximal, the largest one measuring about 41 mm., situated on the under surface of the leaflets; when it matures, rosy-red or purplish in colour, with many fine longitudinal ridges; a transverse exit is made on the proximal end, then a longitudinal slit spreads to its distal end, from which the alate female (fall migrant) flies off.

Syntype: slide specimens collected by the authors in 1942 and mounted in balsam are preserved in the Entomology Laboratory, College of Agriculture, National University of Chekiang.

Habitat: Meitan (Kweichow).

Host: primary host, *Rhus punjabensis* var. *sinica* Rehd. & Wils. Galls on the leaflets.

Macrorrhinarium gen. n.

Antennae short, less than the combined length of head and thorax, 6-jointed, the 3rd and 4th joints short, subequal in length, the 5th and 6th joints moderately long, also subequal in length, the 5th or 6th joint subequal to the 3rd and 4th combined, anterhinial short, each joint with a very large sensorium, as in the genus *Meitanaphis*, with or without inconspicuous setae. Head nearly rectangular, slightly concave on the middle of the anterior margin, broader than long; ocular tubercle present; ocelli large, 3 in number; rostrum short, extends nearly to 2nd coxae. Fore-wing ample, media simple, at the basal half obsolete; stigma normal, short and oblique, not sickle-shaped. On hind-wing both media and cubitus present, with 2 hooklets at the costa; cornicles wanting; cauda small and round; legs slender, long. Both head and mesonotum with wax gland-plates.

Apterous form with 5-jointed antennae and eyes of 3 facets; the antennae of newly hatched larvae 4-jointed.

Genotype: *Macrorrhinarium ovogallis* sp. n.

This resembles *Meitanaphis*, but differs from it in having short oblique stigmata.

Macrorhinarium ovogallis sp. n. (fig. 4).

Fall migrant (winged viviparous female): body dusky green, oblong; antennae 6-jointed, shorter than the head and thorax combined; the 1st and 2nd joints globular; the 3rd and 4th joints short, the latter shorter than the former, the 5th and 6th joints longest, the 6th longer than the 5th; each flagellar joint evenly occupied by a large sensorium sometimes fringed with inconspicuous setae; the remaining sclerotised parts of each joint are formed as a transverse band at each terminal end and a narrow rib through the inner side of the joint; antehinarial short, the length subequal to its width, only $\frac{1}{8}$ the length

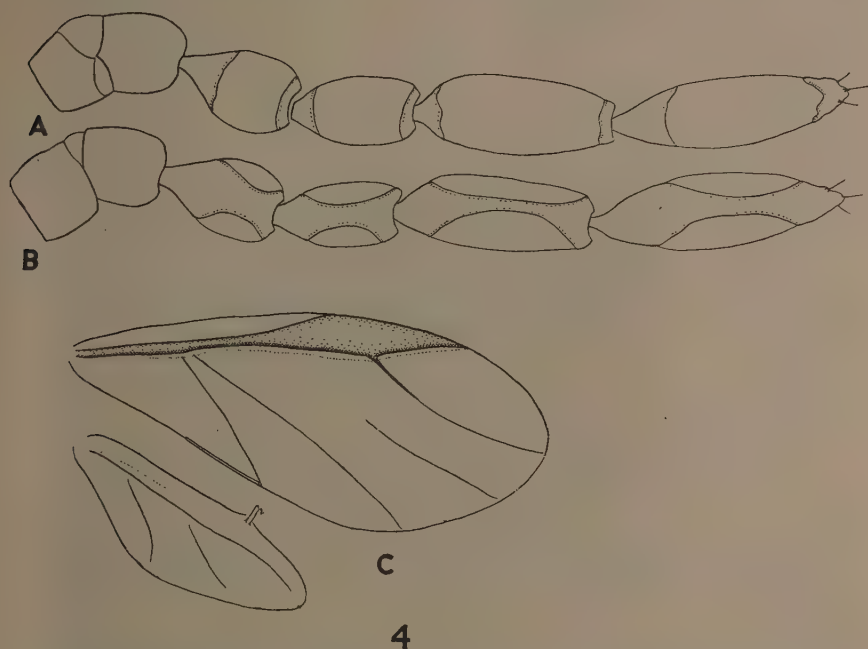


FIG. 4.—*Macrorhinarium ovogallis* sp. n. (Fall migrant). A. antenna (ventral view); B. antenna (dorsal view); C. wings.

and $\frac{3}{8}$ – $\frac{1}{2}$ the breadth of the postrhinial, at the apex with 4–6 hairs. The average minimum breadth of the ribs and the breadth of each joint are represented as follows:—

	I	II	III	IV	V	VI
Average minimum breadth of the ribs (mm.)	—	—	0.016	0.016	0.011	0.014
Average breadth of the joints (mm.)	0.046	0.042	0.034	0.031	0.035	0.030

Head dusky green, slightly concave on the middle of anterior margin; broader than long; with one pair of rudimentary waxgland-plates, sometimes 2 pairs, but more frequently

unpaired; eye dark purple, the ocular tubercle distinct; ocelli purplish-black, 3 in number; antennae greyish with translucent sensoria; rostrum pale green, fuscous distad, extending to between the 2nd and 3rd coxae.

Prothorax pale green, pterothorax greenish fuscous to castaneous brown; mesonotum with a pair of oval waxy plates; wing shining and hyaline, slightly marked with imbrications; stigma of fore-wing fusiform, greenish-grey; veins greenish-brown, stigmatic nervure slightly curved; media simple, subequal to stigmatic nervure, obsolete in basal third; the cubitus and 1st anal veins separate at their bases, the former more slightly curved downward. Radial sector of hind-wing curved at apex; both media and cubitus strong, far paralleled; hooklets 2 in number (occasionally with 1 only or 3); axillaries of both wings pale green. Legs moderately long; tibia less stout than the antennae, with many short setae, fore and middle tibiae subequal, hind one longer.

Abdomen dusky green, with light green at its lateral margins, twice the length of its thorax.

Measurements: length of body 1.5 mm.; width of head (across eyes) 0.33–0.36 mm.; antenna 0.46 mm. (I, 0.039 mm.; II, 0.050 mm.; III, 0.077 mm.; IV, 0.061 mm.; V, 0.110 mm.; VI, 0.130 mm.); length of fore-wing 2.0 mm.; hind leg: femur and trochanter, 0.298 mm.; tibia, 0.413 mm.; tarsus, 0.120 mm.

Nymph of the fall migrant: antennae 6-jointed, pale fulvous, nearly translucent, the apical two joints rather greyish; at the distal end of the 5th joint and the postrhinial each with a round primary rhinarium, the latter with inconspicuously fringed setae; head green; eyes purplish-black; ocelli red; rostrum pale yellow, fuscous distad, extending to between 2nd and 3rd coxae; prothorax and abdomen green, but the latter paler in colour; pterothorax pale turmeric on dorsal and ventral, green on pleural region; legs and wing pads pale yellow.

Measurements: length of body 1.6 mm.; antenna 0.5 mm. (relative length: I, 15; II, 20; III, 20; IV, 21; V, 36; VI, 47); hind leg: femur and trochanter, 0.258 mm.; tibia, 0.310 mm.; tarsus, 0.120 mm.

Newly hatched young (laid by fall migrant): body oblong, while alive pale green in colour, eye black; after mounting in balsam (treated in turpentine only) body yellow, eye red, composed of 3 facets; antennae 4-jointed, translucent, the 1st short, 2nd and 3rd longer, subequal in length, the 4th the longest. There is a small round primary rhinarium distally on the 3rd joint, and a larger one distally on the postrhinial, both with fringed setae. Rostrum long, extending far beyond the 3rd coxae, black at its apex.

Measurements: length of body 0.3 mm.; width 0.17 mm.; antenna 0.1 mm. (relative length: I, 6; II, 8; III, 8; IV, 14); hind leg: femur and trochanter, 0.051 mm.; tibia, 0.068 mm.; tarsus, 0.028 mm.

Fundatrigeniae (apterous viviparous females): body oval, purplish-brown; antennae 5-jointed, pale grey, almost translucent; at the distal end of the 4th and at the postrhinial each with a small round primary rhinarium, the latter one with conspicuously fringed setae. Eye small, black, composed of 3 facets. Rostrum extends near to the 3rd coxae, fuscous distad; legs translucent, with the tibiae a little stouter than the antennae.

Measurements: length of body 1.0 mm.; width 0.8 mm.; antenna 0.3 mm. (relative length: I, 14; II, 16; III, 19; IV, 22; V, 35); hind leg: femur and trochanter, 0.241 mm.; tibia, 0.275 mm.; tarsus, 0.103 mm.

Galls: egg-like in form, sometimes more or less elongate or with a shallow furrow; the size variable, probably due to the individuality of hosts or aphids; mature gall measuring about $69 \times 49 \times 39$ mm., the smallest one being $11 \times 10 \times 6$ mm. only; immature galls are pale green in colour, after mid-stage becoming deeply green with reddish fibrillar veins, and the surface which is exposed to direct sunlight is pale fulvous or red-brown. On splitting, a transverse slit is made on the proximal end of the gall, sometimes continuously slit towards its apex, like a flower; from the opening the alate migrants escape.

Syntype: slide specimens collected by the authors in 1942 and mounted in balsam are preserved in the Entomology Laboratory, College of Agriculture, National University of Chekiang.

Habitat: Meitan (Kweichow).

Host: primary host, *Rhus punjabensis* var. *sinica* Rehd. & Wils. Galls produced on leaflets.

***Macrorhinarium ensigallis* sp. n. (fig. 5).**

Fall migrant (winged viviparous female): closely allied to *M. ovogallis*, but differs from it in the following points:—

1. Antennae much longer and slender, subequal to the combined length of head and

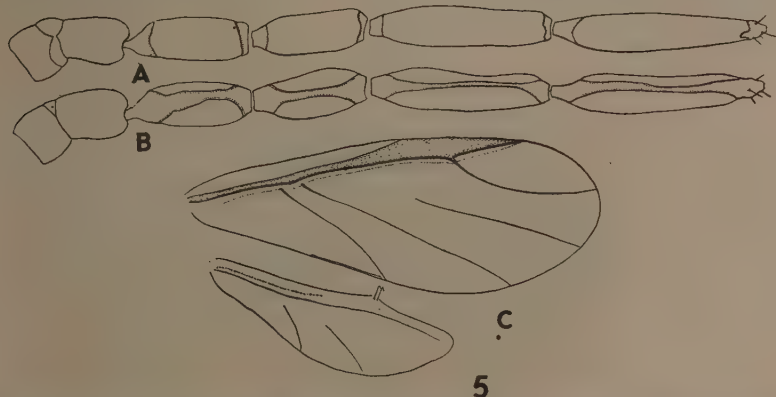


FIG. 5.—*Macrorhinarium ensigallis* sp. n. (Fall migrant). A. antenna (ventral view); B. antenna (dorsal view); C. wings.

thorax. The sclerotised rib of each joint is narrower and always broken on the apical two joints; the average breadth of each joint and of their ribs is represented as follows:—

	I	II	III	IV	V	VI
Average minimum breadth of the ribs (mm.)	—	—	0.0088	0.0069	0.0043	0.0056
Average breadth of the joints (mm.)	0.048	0.042	0.038	0.035	0.034	0.032

2. Anterhinarial much shorter and smaller, the length less than its width, only $\frac{1}{17}$ the length and $\frac{2}{3}$ the breadth of the postrhinarial.

3. The waxgland-plates on the head are 4 in number; more developed than those of *M. ovogallis*.

Measurements: length of body 1.5 mm.; width of head (across eyes) 0.31–0.36 mm.; antenna 0.64 mm. (I, 0.048 mm.; II, 0.057 mm.; III, 0.100 mm.; IV, 0.094 mm.; V, 0.154 mm.; VI, 0.177 mm.); length of fore-wing 2.2 mm.; hind leg: femur and trochanter, 0.337 mm.; tibia, 0.525 mm.; tarsus, 0.132 mm.

Fundatrigeniae (apterous viviparous females): body oval in form; antennae 5-jointed, at the distal end of the 4th joint and of the postrhinarial each with a small round primary rhinarium; rostrum extends far beyond the 2nd coxae, fuscous distad.

Measurements: length of body 1.3 mm.; antenna 0.32 mm. (relative length: I, 15; II, 15; III, 20; IV, 24; V, 39); hind leg: femur and trochanter, 0.218 mm.; tibia, 0.228 mm.; tarsus, 0.090 mm.

Galls: the size is variable, spindle-shaped, the distal end slender and gradually sharp, with a curved hooklet process at its apex; the largest mature gall encountered measured about 100×40 mm., the smallest one, about 30×10 mm. only. Immature gall green in colour; on approaching maturity it becomes yellowish-green. On cracking, a transverse slit is made on its proximal end, and then a continuous slit towards its apex.

Syntype: slide specimens collected by the authors in 1942 and mounted in balsam are preserved in the Entomology Laboratory, College of Agriculture, National University of Chekiang.

Habitat: Meitan (Kweichow).

Host: primary host, *Rhus punjabensis* var. *sinica* Rehd. & Wils. Galls produced on leaflets.

Floraphis gen. n.

Antennae short, less than the combined length of head and thorax, 6-jointed, the 4th joint shorter than the 5th; the latter shorter than the 3rd, the 6th being the longest; all the joints with several incomplete rings, fringed with setae, antehinarian conical and short; head straight on anterior margin, broader than long; ocular tubercle present; ocelli large; rostrum short, reaching somewhat beyond the 2nd coxae; fore-wing ample, stigma long, lanceolate, abruptly oblique, stigmatic nervure opens near the middle of it, media simple, obsolete at the base; the first 2 obliques distinctly separated from each other at the bases; hind-wing with 2 obliques, also widely separated from each other at the bases, with 2 hooklets at the costa; cornicles wanting, cauda round; legs moderately long; waxgland-plates of head and mesonotum both present.

Apterous form with 5-jointed antennae and eyes of 3 facets; newly hatched larvae with 4-jointed antennae.

Genotype: *Floraphis meitanensis* sp. n.

Floraphis meitanensis sp. n. (fig. 6).

Fall migrant (winged viviparous female): body oblong, yellowish in colour; antennae 6-jointed, shorter than the combined length of head and thorax, the 1st two joints globular in form, the rest subcylindric; the 6th joint being the longest, a little less than twice as long as the 4th, the 5th longer than the 4th yet shorter than the 3rd; the 3rd with 4, and the rest each with 3, broad incomplete rings (III, variable 2-5; IV, 1-4; V, 2-4; VI, 3-4), all the sensoria fringed prominently with setae; antehinarian short, the length subequal to its breadth, only $\frac{1}{2}$ the length and $\frac{3}{8}$ the breadth of the postrhinarian, at the apex with 4 short hairs.

Head black in colour; vertex straight, pale blue, with a pair of small waxgland-plates; frons dusky green; clypeus milky; rostrum milky, extending to the 2nd coxae; antennae pale fulvous; ocelli 3 in number.

Prothorax pale green, pterothorax somewhat turmeric, its sternum darker than the alinotum, mesonotum with a pair of large oval waxgland-plates; wing shining and hyaline, more inconspicuously marked with imbrications; stigma of the fore-wing dusky green, darker at its hind margin, long, lanceolate in form, all veins brown, stigmatic nervure darker and stouter proximally; media simple, a little longer than stigmatic nervure, obsolete basally; the cubitus and 1st anal vein separated at the bases, both slightly curved downward; radial sector of hind-wing straight, both media and cubitus present, separated at the bases; hooklets 2 in number (1 or 3 occasionally). Axillaries of wings green; legs

greyish-yellow, moderately long, tibiae as stout as the antennae, with many short setae; fore and middle tibiae subequal, hind one longer.

Abdomen pale yellowish, green at its lateral region, twice the length of the thorax.

The above description of coloration was based upon the newly emerged adults.

Measurements: length of body 1.1 mm.; width of head (across eyes) 0.26–0.28 mm.; antenna 0.44 mm. (I, 0.037 mm.; II, 0.047 mm.; III, 0.093 mm.; IV, 0.063 mm.; V, 0.075 mm.; VI, 0.114 mm.); length of fore-wing 1.8 mm.; hind leg: femur and trochanter, 0.281 mm.; tibia, 0.367 mm.; tarsus, 0.093 mm.

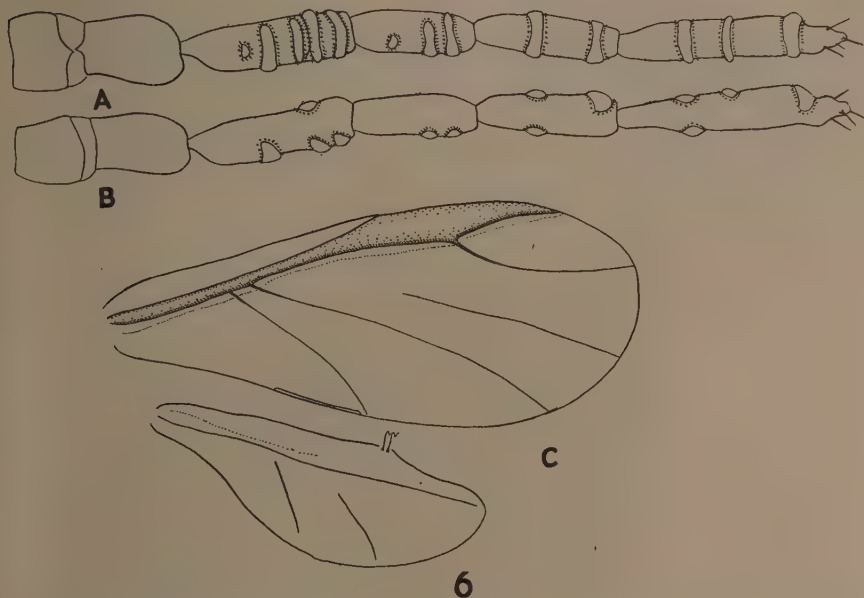


FIG. 6.—*Floraphis meitanensis* sp. n. (Fall migrant). A. antenna (ventral view); B. antenna (dorsal view); C. wings.

Nymph of the fall migrant: antennae 6-jointed; at the distal end of the 5th joint with a small round, fringed, primary rhinarium, at that of postrhinarial a large oblong fringed one, which is transverse in its position. Balsam mounted specimens (treated in turpentine only) showed reddish-black eyes and red ocelli; body pale yellow, appendages paler; rostrum pale yellow, reaching the 2nd coxae, fuscous distad.

Measurements: length of body 1.1 mm.; antenna 0.39 mm. (relative length: I, 15; II, 21; III, 25; IV, 20; V, 23; VI, 37); hind leg: femur and trochanter, 0.232 mm.; tibia, 0.241 mm.; tarsus, 0.077 mm.

Fundatrigeniae (apterous viviparous females): body greenish fulvous, oval or pear shaped; eye black (reddish-purple in balsam mounted specimen); rostrum fuscous at its distal end and extending beyond the 3rd coxae; legs and antennae pale, nearly translucent. Antenna 5-jointed, at the apex of the 4th joint with a small round primary rhinarium and of 5th, with a large oblong primary rhinarium—all of these fringed.

Measurements: length of body 0.61–0.70 mm.; width 0.40–0.52 mm.; antenna 0.23 mm. (relative length: I, 12; II, 15; III, 16; IV, 12; V, 26); hind leg: femur and trochanter, 0.172 mm.; tibia, 0.172 mm.; tarsus, 0.069 mm.

Newly hatched young (found in gall) : body oblong, after mounting in balsam assumes a yellow colour, eyes composed of 3 facets, reddish-black ; rostrum long, extending far beyond the 3rd coxae, tip of the rostrum fuscous ; antennae 4-jointed, on the 3rd joint with a small round, and the 4th with a big oblong, primary rhinarium, both fringed.

Measurements : length of body 0.396 mm. ; antenna 0.16 mm. (relative length : I, 9 ; II, 12 ; III, 16 ; IV, 21) ; hind leg : femur and trochanter, 0.107 mm. ; tibia, 0.096 mm. ; tarsus, 0.054 mm.

Galls : irregularly branched from the base, somewhat flat, rose red, exits being made at each base of the branch or on the side of the galls. A large one measures about 100 by 100 mm. The galls occur on the leaflets.

Syntype : slide specimens collected and sent us by T. C. Hsu in 1942 and mounted in balsam are preserved in the Entomology Laboratory, College of Agriculture, National University of Chekiang.

Habitat : Meitan (Kweichow).

Host : primary host, *Rhus punjabensis* var. *sinica* Rehd. & Wils. Galls produced on leaflets.

Vol. 97. Part 17. Pp. 419-442, 2 pls., 17 figs. 20th November, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

- X DUFFY, Evelyn A. J., F.R.E.S. A contribution towards the biology of *Prionus coriarius* L. (Coleoptera, CERAMBYCIDAE) 419-442, 2 pls., 17 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 9s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.
C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.
H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., PH.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., PH.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., PH.D.

B. M. HOBBY, M.A., D.PHIL.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., PH.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939.

Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Biology War Committee.

Prof. P. A. Buxton, M.A., F.R.S., appointed 1941.

8. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

9. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

Copy

Bind in

28, Lansdowne Road,
East Croydon,
Surrey.

10.6.48.

Dear Miss Evans,

I have referred to my MS. and notes concerning my paper on Prionus coriarius L. as promised, and submit herewith the respective amendments.

P. 433, line 7, for 'day', read 'week'.

line 33, for 'day', read 'week'.

line 39, delete 'or four'.

P. 435, line 12, for 'directly', read 'may', and
delete 'or diminish'.

As these errors are undoubtedly due to carelessness on my part, I apologise for the inconvenience I have caused you.

Yours sincerely,

(Sgd.) E.A.J. DUFFY.

A CONTRIBUTION TOWARDS THE BIOLOGY OF *PRIONUS* *CORIARIUS* L. (COLEOPTERA, CERAMBYCIDAE)

By Evelyn A. J. DUFFY, F.R.E.S.

Manuscript received 25th April, 1946.

(Read 2nd October, 1946.)

WITH PLATES 1 & 2 AND 17 TEXT-FIGURES.

CONTENTS.

	PAGE
Introduction	419
Acknowledgements	420
The Adult	420
The Egg	422
The Larva: General Description of Prionine Larvae	422
The Larva—Final Instar	423
The Larva—First Instar	428
The Larva—Later Instars	430
The Pupa	431
Habits of the Adult	432
Emergence	432
Feeding Habits	432
Attraction to Light	432
Stridulation	432
Copulation	433
Oviposition	433
Months of Emergence and Duration of Adult Existence	433
Flight	433
Habits of the Larva	434
Pupation	435
Edibility of Larva	436
Resistance of Larva to Drowning and its Reaction to Low Temperatures	436
Parasites and Natural Enemies	437
Methods of Preservation	437
Habitats	438
Collecting and Rearing Methods	439
Economic Importance	440
Distribution in Great Britain	440
Status of Colonies	440
References	441

INTRODUCTION.

INFORMATION concerning various aspects of the species under discussion is extremely scattered and a number of contradictory statements, especially with regard to pupation, habits of the larva, etc., have been published from time to time. Furthermore, details and descriptions of the first and early larval stages, habitats and many other factors are not available. The transformations

of *Prionus coriarius* L. were first discussed by Rösel von Rosenhof (1746) and, later, by Planet (1891), but both these accounts are incomplete.

The present author has attempted to correlate all the reliable facts and records, to which he has added his own experiences and observations. The latter would not have been possible but for the recent discovery of numerous larval colonies, which afforded an admirable opportunity for field observation and provided ample larval material.

Eggs, larvae and pupae have been presented to the British Museum (Natural History).

ACKNOWLEDGEMENTS.

The author wishes to express his gratitude to Dr. K. G. Blair for reading through this paper, and to Dr. F. I. van Emden for his invaluable criticism of the passages concerning larval taxonomy. Dr. D. A. B. Macnicol very kindly undertook to photograph the material obtained by the author (Plates 1 & 2), while Dr. R. C. Fisher, of the Forest Products Research Laboratory, has been good enough to furnish information regarding the economic importance of *Prionus*. Thanks are also due to Professor G. D. Hale Carpenter, Messrs. C. MacKechnie Jarvis, R. R. U. Kaufmann, P. M. Miles, and to all those who kindly sent references and records of distribution.

THE ADULT.

The subfamily PRIONINAE of the CERAMBYCIDAE is a large one comprising over two hundred genera. Fowler (1890) states "... they are distinguished



FIG. 1.—*Prionus coriarius* L. : dorsal view of female (natural size).

by their connate and obsolete labrum, margined thorax, and produced prosternum; the anterior coxae are transverse and distant, with the cavities open behind, and are furnished with linear trochanters; the mandibles are strong, incurved at apex; the thorax is somewhat indistinctly margined, and is strongly spined at sides; the femora are long and not clavate; the general form is large and more or less depressed, the elytra being as a rule somewhat coriaceous in appearance; the first segment of the abdomen is not or scarcely longer than the second; the first three joints of the tarsi are broad and are strongly pubescent on their under side."

Six genera are represented in Europe; of these *Prionus* Geoffroy comprises three European species, only one of which (*P. coriarius* L.) is indigenous in

Britain. This insect, which is the largest British longicorn, has broad, leathery elytra, conspicuous thoracic spines, and long, rather stout legs (fig. 1). The thick antennae, which are strongly serrate in the male, are undoubtedly its most attractive feature. Its popular name is the Tanner Beetle, so called on account of its leathery elytra.

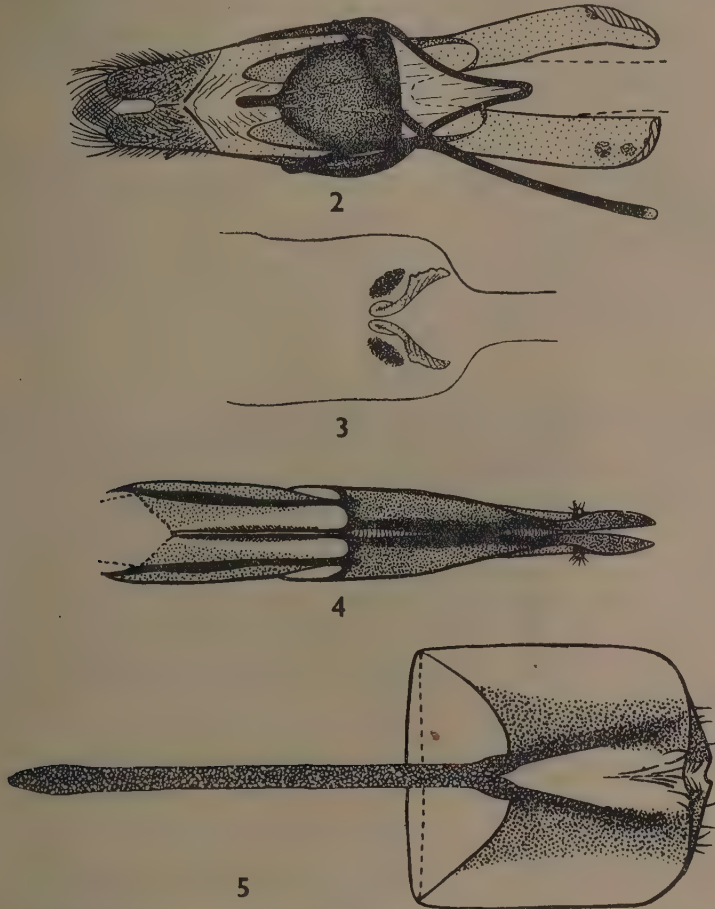


FIG. 2.—Male genitalia of *P. coriarius* L., showing median lobe, median struts, tegmen and tegminal strut ($\times 15$).

FIG. 3.—Male genitalia of *P. coriarius* L., showing internal sac ($\times 15$).

FIG. 4.—Female genitalia of *P. coriarius* L., showing specialised tube ($\times 7$).

FIG. 5.—Female genitalia of *P. coriarius* L., showing sheath and rod of ovipositor ($\times 10$).

The following specific description is given by Fowler (1890) :—

“ A very large and conspicuous species, oblong, rather depressed, slightly shining; without pubescence on upper side, of a pitchy black or dark, pitchy brown in colour, underside usually more or less castaneous, with the breast rather densely pubescent; head rather small, with long, projecting mandibles, eyes transverse, not strongly marginate;

antennae long and robust and strongly serrate in males, shorter and less serrate in the females. Thorax transverse, sinuate at base, much narrower than elytra, spined at sides, rugosely punctured, scutellum rounded behind; elytra broad, rugosely punctured with obsolete traces of raised lines, indistinctly mucronate at sutural angles; legs rather long and stout, femora and tibiae compressed. L. 25–38 mm.

Male with antennae distinctly 12-jointed, longer, more robust and more strongly serrate, abdomen pubescent, fifth segment depressed and slightly emarginate at apex.

Female with the antennae 11-jointed, the last joint being obsoletely 3-jointed, shorter and less strongly serrate, abdomen glabrous, fifth segment very slightly emarginate at apex."

This species varies considerably in size, the males usually being the smaller; a variation of 23–44 mm. has been found in preserved specimens examined by the author.

Various monstrosities have been recorded, notably those by Krause (1888) and Schneider (1884).

The male and female genitalia (figs. 2–5) have been drawn from slide material prepared by the author. No remarks seem necessary except that the male testes have six sperm tubes.

THE EGG.

The eggs are attached to the bark in batches by a quick-drying fluid, which is secreted from a gland and spread by the ovipositor as they are forced out.

In form they are elongate-ovoid with rounded ends, the posterior pole being slightly attenuated (Plate 1). When first deposited the egg is almost white, becoming light-brown later, and, if the secretion has been applied thickly, slightly shining as though varnished; but often the secretion fails to cover the egg completely and leaves dull patches. The average dimensions of twelve eggs were 4.1 mm. long by 1.4 mm. at their greatest width. The chorion is opaque, exceedingly thick and coarsely reticulated, each polygonal area being depressed and having a minute, though deep puncture in the middle. It has proved to be impervious to some fluids. On one occasion, for instance, a few eggs were immersed in 40% formalin for one hour and allowed to dry—and larvae emerged a week later.

Under laboratory conditions the period of incubation has varied from 30 to 37 days, the average temperature being 60 deg. F.

THE LARVA.

General Description of Prionine Larvae.—Larvae of the PRIONINAE may be distinguished from those of other subfamilies of the CERAMBYCIDAE by the following key, which has been extracted from a paper by Craighead (1915):

"Head transverse, broader than long.

Epistoma projecting over clypeus; front projecting over epistoma, dentate or carinate (except *Parandra*); clypeus as wide at base as epistoma; mandibles acute. Legs present PRIONINAE.

Epistoma not projecting; front smooth and rounded. Mandibles acute; clypeus occupying space between condyles.

Sides of epicranium meeting behind front, fused for some distance, then separating. Dense brush of hairs on gena behind pleurostoma. Ninth abdominal segment bearing a pair of chitinous spines. Form cylindric

ASEMINAE.

Sides of epicranium meeting behind front, then separating (not fused), angulate. Caudal spines usually absent. Lateral zone usually distinct on all abdominal segments. Form depressed LEPTURINAE.
 Mandibles with cutting edge rounded (gouge shaped). Clypeus not as wide at base as epistoma CERAMBYCINAE.
 Head oblong, sides parallel or narrowing behind.
 Clypeus as wide at base as epistoma; mandibles obliquely acute. Sides of epicranium behind front fused for entire distance. Legs absent (rarely present) LAMINAE."

In Britain we have only one representative of the subfamily (*P. coriarius* L.), the larva of which possesses the following combination of characters:—¹

Head: Front margin of frons with a more or less straight, keel-shaped upper boundary; lower boundary produced over clypeus in four lobes² (one lateral and one paramedian pair); three pairs of epistomal setae present; clypeus transverse (as wide as front margin of frons); labrum transverse; antennae with minute apical (third) segment.

Thorax: Anterior half of pronotum with a conspicuous transverse band of darker pigment, posterior half irregularly rugose.

Abdomen: Ampullae finely rugose³; pleural discs present on segments 1–6.

Final Instar.—This stage of the larva has been dealt with by Rösler von Rosenhof (1746) and even by Latreille, who considered the prothorax to be a part of the head. It has been more recently described and illustrated in detail by Schiödte (1876), but a comparison with British material showed that the sculpturing of certain structures (*e.g.* the frons and labrum) in his figures was distorted in appearance. This may possibly be due to geographical variation in the larvae.

The full-grown *Prionus* larva (Plate 1) is a soft, fleshy grub, sub-cylindrical and, like most Cerambycid larvae, broadest at its prothorax and narrowed posteriorly. It is of a smooth texture, and sparsely hairy. The general colour is pale yellowish-white (the ninth segment often being greyish-white, due to its greater transparency revealing the hind gut), and it has a waxy appearance. The head is armed with powerful mandibles, while its abdominal muscles are well developed. The final stage larva varies in length from about 65 to 75 mm. The average head-width of six mature larvae was found to be 9.2 mm.

Head: The head is slightly transverse, wider behind the middle, and capable of being considerably retracted into the prothorax. It is strongly sclerotised, especially the exposed portion which is more or less darkly pigmented. The dorsal surface (fig. 6) comprises two slightly rugose epicranial halves which are separated by the triangular frons; the margins of the former fuse for a short distance behind the frons, and then diverge. The strongly-shouldered genae are darkly pigmented, rugose, and bear a few isolated setae of various lengths.

The frons consists of three differently pigmented areas; a narrow, pitchy, anterior margin, merging posteriorly into a ferruginous area, which in turn gradually merges into a testaceous area. The last is smooth, but the median ferruginous area bears a series of rugose furrows which converge posteriorly towards the fine, though well-defined, median suture which bisects the frons. Immediately behind the anterior margin are three pairs of conspicuous setae. The frons is bounded on two sides by the pale, rather indistinct,

¹ These have been mainly adapted from van Emden's key (1939).

² This character has been found to vary, and is discussed in detail in the section concerning later instars.

³ This is more apparent in later stages.

frontal sutures which extend forward to the outer part of the antennal ring. On the frons, immediately behind the dorsal articulation of the mandible, is a curved, shallow depression bearing three setae and bounded posteriorly by a slightly crenulate ridge. The front margin of the frons (or epistoma) lies between the dorsal mandibular articulations, and possesses important generic characters. It is a pitchy, heavily-sclerotised ridge, abruptly sloping and bearing on each side three small epistomal setae: its upper boundary is slightly curved (in some specimens almost bilobed), keel-shaped, and with a median depression; its lower boundary is produced over the clypeus in four rugose lobes, *i.e.*, one large, pointed lateral pair, and one smaller, usually less pointed, paramedian pair.⁴

Anterior to the front margin is the clypeus, a white, glabrous membrane; this is trapezoidal in form (roughly five times as wide as long) and as wide at base as the epistoma, beneath which it is partially retractile.



FIG. 6.—Larval head of *P. coriarius* L., final instar, dorsal view ($\times 10$ circ.).

Attached to the clypeus is the labrum: this is a thick, coriaceous, almost semi-circular organ, which is twice as wide as long. It is testaceous and covered with rather stout, reddish setae, except the basal region, which is almost glabrous and more darkly pigmented.

The powerful triangular mandibles are produced, the acute cutting edge being broadly and obliquely emarginate. They are strongly rugose on their outer face, but the upper inner face is almost smooth. Their apical half is dull, the basal half shining, and they are wholly pitchy.

The robust antennae are partially retractile, and consist of three segments. The first segment can be partially retracted into the rather broad, pale, basal membrane; the second joint is barrel-shaped, its apex being obliquely truncated, bearing a minute oval

⁴ The variation of this structure is discussed in the section on Later Instars.

sensory organ and a dome-shaped third joint which has three minute apical setae (fig. 7). All three joints are ferruginous. The antenna is protected on its inner-dorsal side by a projecting sclerotised ridge. There is no indication of the presence of ocelli in this species.

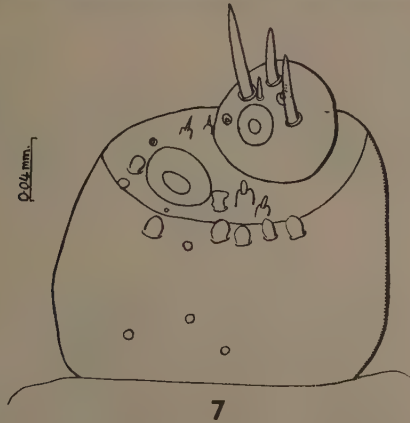


FIG. 7.—Larval antenna of *P. coriarius* L., final instar; second and third segments of left antenna, ventral view.

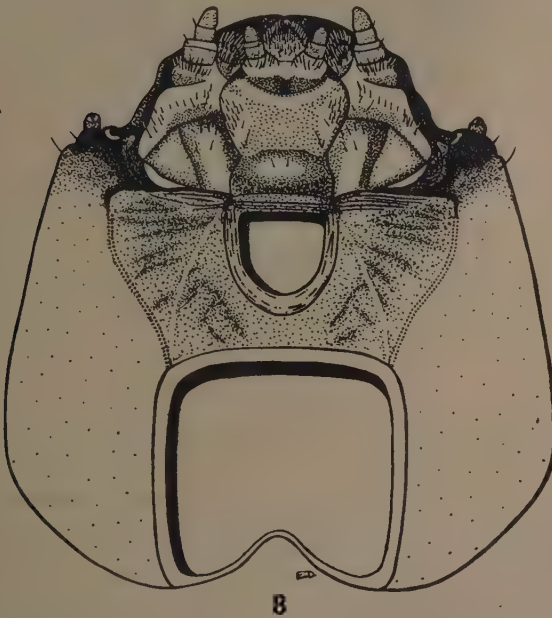


FIG. 8.—Larval head of *P. coriarius* L., final instar, ventral view ($\times 10$ circ.).

On the ventral portion of the epideranium, just behind the ventral articulation of the mandible, is a sharply produced, conical process.

The ventral mouthparts are exceptionally large, fleshy and leathery (fig. 8). The

lateral sutures of the gula diverge to meet the anterior portion of the occipital foramen, which is divided into a small anterior and a larger posterior portion by the trapezoidal, transverse tentorial cross-arm. The ligula is cordate, fleshy, and is densely covered with short, bristly setae; on either side are the two-jointed, robust, labial palpi which have a dome-shaped apical joint.

The maxillae are completely free and movable, the cardo, articulating sclerite, and stipes being robust and fleshy. The maxillary lobe is densely covered on its inner side with rather long, reddish setae. The three-jointed maxillary palpi (fig. 9) are robust, the first joint being strongly transverse, the second quadrate, and the apical joint, which is slightly elongate and bluntly conical, truncate at the tip.



9

FIG. 9.—End of right maxilla (ventral view) of larva of *P. coriarius* L., final instar.

Thorax: Apart from the head, the prothorax is the most strongly sclerotised and pigmented part of the body, and bears scattered setae of various lengths. It is very large, being longer than the meso- and metathorax combined. The rectangular pronotum is delimited laterally by a pair of conspicuous grooves, and is bisected by a shallow, though distinct, longitudinal, median furrow (fig. 10). This plate comprises two diversely sculptured areas, the anterior one being more or less transversely rugose and bearing a few scattered coarse setae, and the posterior one being more strongly and irregularly rugose and glabrous. Its shining, milky-white colour presents a strong contrast with the rest of the body. The most conspicuous feature is the narrow, ferruginous, transverse band which traverses the anterior third of the prothorax, and touches the extremities of the lateral furrows; this

band is divided into two halves by the median suture. Anterior and parallel to this are four small, ferruginous, elongate areas (one lateral and one paramedian pair). The mesonotum and metanotum are much shorter; each is divided by two oblique sutures which fuse medially, forming in the former a V, and in the latter an inverted V.



10

FIG. 10.—Larval prothorax of *P. coriarius* L., final instar, dorsal view ($\times 6$ circ.).



11

FIG. 11.—Lateral view of first abdominal segment of larva of *P. coriarius* L., final instar, showing spiracle and pleural disc ($\times 10$ circ.).

The five-segmented legs, though conspicuous, are comparatively short considering the size of the larva; they are stout and conical, and roughly equal in length to the maxillary palpi. In the prothorax the coxae are contiguous, but in the other two segments they are widely separated. The trochanter is only visible on its inner side. The femur is transverse and has a ferruginous basal half. The tibiotarsus is cylindrical, slightly longer than the femur, and wholly ferruginous on its outer side. The claw is in the form of a long, slender spine, its apical half being ferruginous and sclerotised. With the exception of the coxa and the claw, all the joints bear a fringe of reddish setae on their inner side.

Abdomen: The abdomen is composed of ten segments, the tenth consisting of three lobes which surround the anus. Each segment is divided into a dorsal and a ventral

portion by the ridge-like epipleura, which are markedly protuberant on segments seven, eight, and nine.

On the epipleura of the abdominal segments are small pleural discs which are characteristic of the PRIONINÆ; these are very delicately sculptured, and can be seen only in living larvae or in spirit material that has been allowed to become slightly dry.

In the present species they occur on segments one to six, that on segment one being the most conspicuous (fig. 11), the others becoming less so posteriorly. Each consists of a circular depression in the skin, from which fine, uniform striae radiate to form a regular disc; this disc is surrounded by an irregularly rugose pattern, more or less triangular in shape. Immediately below this disc are two or three long, coarse setae, and a few scattered shorter ones. Segments one to seven are similar in structure and each bears dorsal and ventral ambulatory ampullae. The dorsal ones are large, fleshy, and high-set, giving the larva (especially when fully distended) the appearance of being compressed laterally. Each dorsal ampulla is marked by two transverse, slightly-curved furrows, and a broader, shallow, median, longitudinal furrow, and is limited laterally by a pair of deep, oblique furrows. These ampullae are only slightly rugose, and differ but little from the general body texture; each bears a few short, coarse setae (fig. 12). Ventrally, the



12

FIG. 12.—First abdominal segment of larva of *P. coriarius* L., final instar, dorsal aspect ($\times 15$ circ.).

ampullae are broader and shorter and less protuberant, and bear only one transverse furrow. Surrounding each ampulla is an elliptical, protuberant area which is greatly swollen laterally.

Segments eight and nine are completely smooth. The ninth is by far the longest segment and is not telescoped into the preceding one. The apex of the tenth segment is divided into one dorsal and two latero-ventral lobes (the anal lobes) by three sutures, the dorsal lobe being slightly more protuberant. Each lobe is slightly rugose and bears a few rather long setae.

The spiracles of the larva are ovoid, bilabiate and very conspicuous. The thoracic pair are situated laterally between the pro- and mesothorax. Reddish spiracles occur on the abdominal segments one to eight, the first pair being the largest. Each one is surrounded by a comparatively thick sclerotised rim and is borne on the centre of an elliptical area between the parascutum and the epipleura.

First Instar.—On emergence from the egg the larva measures on an average 5 mm. in length, with a head-width of 0.75 mm. Its general form differs from that of the later instars in that the thoracic segments are less transverse, and the abdominal segments are less tapering posteriorly, the ninth segment being much less elongate. In life the larva is of a waxy appearance and greyish-white in colour (occasionally with a pinkish tendency)—with the exception of the prothorax, which is milky-white. The anterior margin of the frons, and the fine, though well-defined, median suture are ferruginous, the rest of the head capsule being testaceous.

The front margin of the frons bears three pairs of long, slender setae; the lower boundary

scarcely projects beyond the upper boundary, and, apparently, the paramedian lobes of the mature larva in this stage are fused to form a single lobe, the anterior margin of which is slightly curved upwards (a structure closely resembling a rostrum). The lateral lobes are absent.

The clypeus and labrum are white, the latter being slightly transparent and bearing on its inner margin numerous pale setae of varying lengths, some of which are as much as twice the length of the labrum itself. The antennae are testaceous, the apical joint being almost invisible. The mandibles are ferruginous at the base, but are pitchy apically and strongly curved inwards. The genae bear a pair of very long setae.

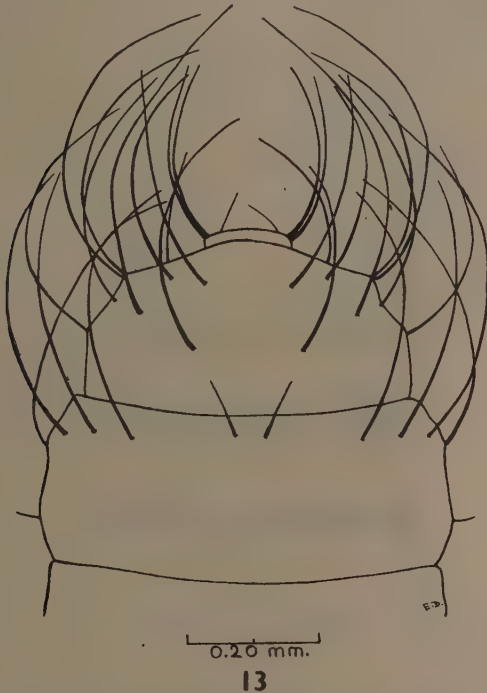


FIG. 13.—Last three abdominal segments of first-stage larva of *P. coriarius* L. (dorsal aspect), showing position and length of setae.

Ventrally, the mouth frame is ferruginous, and the mouthparts testaceous. The sub-fossal spines are strongly produced.

In living specimens, especially, the pronotum is milky-white, the posterior half being irregularly rugose. There is no indication of the ferruginous transverse band so conspicuous in the mature larva. The legs are testaceous and are equipped with a long, slender claw.

The pleural discs cannot be distinguished in this stage, as all the abdominal segments are completely covered with minute tubercles (best seen in living larvae). The epipleura are slightly protuberant on the last three segments!

Although not possessing special egg-bursting spines, as does the first-stage larva of *Aromia moschata* L., *P. coriarius* has, nevertheless, some very long, slender, slightly-curved setae on all the segments, which appear to assist the larva in gaining egress from the egg;

by convulsive, peristaltic movements, the larva has been observed to force itself through the neat, oval orifice (which it has made with its mandibles) at the broader end of the egg, and, as it emerges, the freed setae (previously recumbent) spring to a more or less erect position, thus preventing the larva from going backwards whilst performing its peristaltic motions. The extraordinary length of these setae is shown in fig. 13. Those on the last three segments of the abdomen are the longest and are more strongly curved backwards.

When the greater part of the body has been freed from the egg the larva rests; during this period it attains a more robust appearance, and the head capsule becomes more strongly pigmented. The egg-shells are not eaten.

Later Instars.—In the second stage the abdominal setae are proportionately much shorter; only the lateral pairs maintain their proportional length.

The ampullae are more clearly defined, and are finely rugose. The head capsule becomes darker, and the labrum less transparent and almost testaceous, its setae having become appreciably shorter. Larvae in this stage are usually slightly pink in life. The conspicuous median lobe of the front margin of the frons is now absent, and the lower boundary of the front margin is entirely straight. The clypeus is comparatively large.

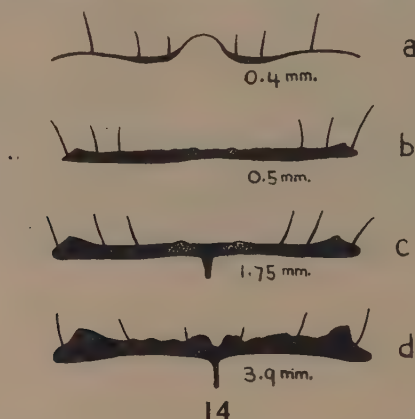


FIG. 14.—Variation in the front margin of frontal piece in various larval instars of *P. coriarius* L.; (a) first instar, (b) second instar, (c) fourth instar and (d) final instar.

The irregular rugosities of the posterior half of the pronotum are more clearly defined. The tarsal claws have become much shorter and stouter. Owing to the general rugosity of the segments, the pleural discs are not yet distinguishable. The spiracles, however, have become visible to the naked eye, the respiratory opening being circular, and surrounded by a conspicuous white rim.

In the third stage the spiracles are still circular, and the pleural discs still indistinguishable. The ninth abdominal segment has become more elongate, and the dorsal abdominal ampullae are now clearly defined.

It is not until the larva has entered its fourth stadium that its systematic characters correspond closely with those of the final stage larva—and even then the frons is not characteristic of the final stage.

The marked variation of a single character from one instar to another in the same species is exemplified by the front margin of the frons of *Prionus* (see fig. 14). In the first instar (a), the upper boundary is produced in the middle beyond the lower one to form one large lobe. In the second instar (b), this lobe is absent but the ridge is more apparent, its two extremities being very slightly produced, and the two small paramedian lobes are

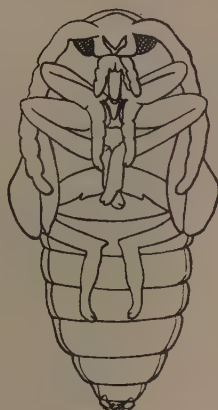
visible between the upper and lower boundaries. By the time the larva has entered its fourth stadium (c), these lobes have developed appreciably, but it is not until the larva is in the second half of its development that both pairs of lobes are well formed (the paramedian pair having merged into the lower boundary), and the entire front margin has become markedly keel-shaped (d).

THE PUPA.

Apart from very brief references to the pupa by Rösel von Rosenhof (1746) and Planet (1891) (who both give outline figures), no description or illustration of this stage of *P. coriarius* could be found in previous literature. In the present paper, outline figures of the dorsal and ventral aspects are included (figs. 15 and 16).



15



16

FIG. 15.—The pupa of *P. coriarius* L., dorsal aspect.

FIG. 16.—The pupa of *P. coriarius* L., ventral aspect.

The freshly-formed pupa is entirely white, though comparatively dull and of a leathery texture. It is not until at least a month later that pigmentation takes place; the tips of the mandibles are the first parts to exhibit this. It is broad and heavily built and its appendages are easily disarranged. The size, as one would expect, varies considerably. The author has taken pupae varying between 30 and 40 mm., the female specimens being the larger.

Its general form is similar to that of the adult. The head is bent beneath the thorax with its conspicuous mouthparts protruding posteriorly. The short, thick antennae arise on the side of the head immediately above the large eyes, and lie alongside the thorax, passing over the elytra, where they curl slightly downward to terminate more or less in line with the posterior margin of the metathorax. The elytra and wings (which are thick, leathery, and loosely set) lie in a lateral position with their apices slightly diverging. On the disc of the head are four converging series of short striae. The rugose pronotum is marked with long, rather deep, transverse striae, and has a smooth median furrow.

In this stage the lateral thoracic spines of the adult are conspicuous, the middle pair being particularly well developed. The mesonotum is likewise striated, but there is no median furrow; its posterior margin is produced medially into a prominent fleshy lobe, the scutellum. With the exception of a single longitudinal series of short, transverse striae,

the metanotum is smooth. A pair of large, narrow spiracles are placed ventro-laterally on the mesothoracic segment.

Abdominal segments one to six are each equipped with a pair of dorso-lateral spiracles, those on segment one being the largest. Dorsally, all the abdominal segments are strongly rugose, the epipleura especially so. Each segment from one to six bears scattered, short tubercles which are set in a cushioned area (? analogous to the larval ampulla). Segments seven and eight are practically smooth, but the ninth is markedly rugose and bears two paramedian, elongate, fleshy protuberances, which slightly converge posteriorly. The tenth segment, which is telescoped within the ninth, bears a large, fleshy, apical lobe, below which are two smaller more conical ones; these are the sexual organs. With the exception of the last two, all the abdominal sternites are smooth.

To the naked eye or even under a lens, the pupa appears to be totally glabrous (unlike those of the majority of British longicorns which bear conspicuous spines), but if subjected to a high magnification, a few of the tubercles on segments one to six are seen to bear minute, stunted setae. It has been noticed that the larva of *Aromia moschata* L. pupates head-downward and that the dorsal spines of the pupa (which are inclined forward) probably enable the adult to free itself completely from the pupal skin and also serve to keep the pupa *in situ*.

Pupae of many other Cerambycids have since been examined, and it has been found that species the larvae of which pupate head-upward all have pupae with backward-projecting spines. The fact that the *Prionus* pupa is entirely devoid of these spines is another indication that its larva does not naturally pupate in the wood (see "Pupation").

HABITS OF THE ADULT.

Emergence.—As soon as the adult is fully hardened and pigmented it ruptures the soft earthen cell and forces itself through the inch or so of soil above it into the open air, leaving behind it a conspicuous hole in the earth. These emergence holes often provide a useful indication of the presence of a larval colony or even pupae. The author has on several occasions seen these holes, which usually occur alongside the exposed parts of the tree's roots: on one occasion nine were seen around the base of a single tree, their average diameter being roughly one inch.

Feeding Habits.—Although adults do not appear to feed on foliage, wood, or flower-heads, there have been several records of their being attracted to entomologists' sugaring posts; for example, a female was taken at "sugar" on a birch tree in 1945 by E. W. Classey, and two males and a female were caught in similar circumstances by W. West. A female under observation was provided with diluted honey, but it could not be induced to feed on it.

Attraction to Light.—This insect is occasionally attracted to light, but this would appear to be greatly influenced by weather conditions. Hunt (1914) took two specimens, both of which had been attracted to an arc-lamp, and there is a more recent record of one flying to light by Pinhey (1935).

Stridulation.—As stated later on, this beetle stridulates loudly, especially when molested or while engaged in copulation. The rasping sound is produced by repeatedly raising and lowering the forepart of its body, which causes the sharp, downward-bent, posterior margin of the pronotum to rub against a series of minute, transverse ridges which lie on a circumscribed area on the mesonotum. The sound is likened by certain authors to that produced by the Death's Head Hawk Moth (*Acherontia atropos* L.).

Copulation.—It is remarkable how active this rather sluggish species can become, especially when about to engage in copulation. The male almost springs on to its prospective mate, often at the same time having to ward off persistent rivals. The males are ferocious fighters, and with their exceptionally well-developed mandibles can inflict severe injury upon one another, such as biting off legs and antennae.

Pairing, which commences a ~~day~~ or two after the adults have emerged, usually takes place on boles or branches between the hours of dusk and midnight, though pairs in *copula* have occasionally been seen in the daytime. Prior to the act, the female adopts a resting position, its fore legs being extended in front while the middle and hind legs lie posteriorly, away from the body. Any attempt on the part of the female to evade the male's embrace is usually overcome. During copulation these beetles stridulate loudly, the sound being audible some yards off.

The male embraces its mate's abdomen with its front legs, which are crossed beneath it a little in front of the posterior femora, its middle legs crossing behind them. Its posterior legs are directed behind to embrace the sides of the pygidium and ovipositor, its tarsi being supported by the female's abdomen. The male then bends its pygidium to meet the ovipositor and quickly extrudes its genital tube, which it inserts into the vagina. Throughout the act, which lasts only a few minutes, the male's trembling antennae are directed forwards, while its palps continually rub the thorax of the female. Both males and females have been observed to copulate with several mates.

Oviposition.—Oviposition usually begins at night two or three days after copulation. By means of the powerful ovipositor the eggs are inserted deeply into crevices in the bark, usually at the base of trunks or in partly exposed roots, at the average rate of three or four a minute. They are deposited one against the other in batches of 8-12 in one place. In one female observed, 40 eggs were deposited (roughly in batches of 9) on a piece of bark on 21st July, 1945; it died the day after, and, upon dissection, its abdomen was found to contain 108 soft, pale, rather viscous eggs. Fowler (1890) records the capture of a female containing 162 eggs. Oviposition usually takes two to three days; the females generally die a ~~day~~ or two after.

Months of Emergence and Duration of Adult Existence.—This species usually emerges rather later than the majority of British longicorns, often not appearing until mid-July. June records, however, are not uncommon, and two males were taken in the New Forest in May by W. West.

The males are usually the first to emerge, and appear to be shorter lived than the females, as they seldom survive for more than three ~~or four~~ weeks. The peak period of emergence is August; after this month the numbers gradually decline, though records of captures as late as October are by no means infrequent.

Adults have been found from time to time at roots of old oaks in winter; they go down apparently to shelter themselves from the cold, and often die there, as dead specimens are very frequent. This prolonged survival would seem to be due to two factors: a late emergence (*i.e.* September or October), and absence of severe frosts. There is no evidence that the species hibernates.

Flight.—This species, particularly the males, sometimes indulge in large-scale flights which appear to take place usually on warm, sultry, or even wet evenings during the peak period of emergence. On one evening in July 1937 E. W. Classey, who was collecting Lepidoptera on Esher Common, saw thirty

to forty adults flying between dusk and midnight; incidentally, on this occasion not a single specimen was attracted to "light" or "sugar."

According to F. Haines, a neighbour of his observed that numbers of adults flew over a bed of *Cosmos* in his garden at dusk on a warm August evening. In publications of the last century may be found vivid descriptions of enormous swarms of these insects which "obscured the twilight sky."

An observation regarding this insect's flight, which seems neither conclusive nor convincing, has been made by Marié (1924). Apparently he saw a *Prionus* flying on several consecutive evenings at the same time and place and suspected that it was the same beetle—as on each occasion it was a male that he saw! "Cette observation," he continues, "semblerait prouver qu'après leur vol crépusculaire les *Prionus* sont capables de revenir à leur point de départ, que ce point soit l'endroit de leur éclosion ou tout autre lieu."

The flight of *Prionus* is, as would be expected, moderately fast, deliberate and heavy, and is seldom very high.

Although this insect is seen more frequently at dusk, it is by no means entirely crepuscular. For instance, Mr. A. H. Turner, in a letter to the author, mentions that on one occasion at Dereham adults advertised themselves by flopping on to a corrugated iron roof between midnight and 4 a.m. (D.B.S.T.).

HABITS OF THE LARVA.

As soon as the first-stage larva has emerged it begins to gnaw its way into the bark. According to Rösel von Rosenhof (1746), the egg-shells serve to block up the opening of the tunnel, thus preventing the frass from falling out and providing purchase for the larva to burrow in farther; but larvae appear to be quite capable of entering without this assistance. Locomotion is secured through the engagement of the well-developed ambulatory ampullae. Until the third or fourth stadium is attained they feed subcortically, and then proceed to bore deeper towards the underground roots, where they remain until ready for pupation. The longitudinal galleries are simple (*i.e.*, without ramifications), extensive, and are packed with coarse, shredded shavings. Burrows up to two yards in length, with a maximum width of just over one inch, have been observed in the field. The individual tunnels are kept strictly separate, and even when they cross older ones they usually pass round rather than through them. Larvae prefer damaged or rotting roots, and when their supply of food is exhausted they travel, if necessary, through the earth to nearby roots. Roots of a diameter of roughly one to four inches have frequently been seen to be almost completely reduced to frass and shavings, nothing but the thin outer covering of bark and sometimes a hard central core being left. It was noticed that the frass in the heartwood of stumps is more tightly packed than it is in the roots. Photographs of a section of a birch stump in which the galleries are tightly packed with frass, a cross-section of a gallery, and a *Prionus*-infested root are shown on Plate 2.

A larva (about two-thirds grown) under observation in a glass tank was seen to construct—or, rather, press out—a large, roomy cell between its pabulum and the bottom of the tank, where it remained motionless for eight days and then underwent ecdysis.

Soon after the final instar is attained, the larva leaves the root and makes its way (if necessary) to within an inch or so below the surface of the earth (see "Pupation," p. 435). In its prepupal stage it becomes somewhat contracted, the intersegmental skin being wrinkled.

In the process of extracting a mature larva from its burrow in solid wood, it was seen to eject forcibly from between its parted mandibles a stream of dark brown fluid for a distance of a few inches. Although this happened on two occasions, repeated attempts to provoke this behaviour in the laboratory failed.

The larvae are voracious feeders and are capable of breaking down four or five times their own bulk of wood within a week.

Although adults have not been reared *ab ovo* during this investigation, larvae have been reared throughout their first three and last two stages, and sufficient larval material has been obtained at various months of the year to indicate that the larval period is at least three years. No doubt temperature, moisture, and availability of food ~~directly increase or diminish~~ this period by a year or possibly two. The larva first undergoes ecdysis about six weeks after its emergence; from then onwards the period between moults would seem to become progressively longer. A one-year-old larva measured only 2.2 cm. with a head-width of 2.9 mm.

Owing to its long life and the fact that close continuous observation is difficult, it has not been possible to ascertain the exact number of larval instars. The following table shows both observed and calculated head-widths, the latter being based on Dyar's Law: the ratio of increase has been obtained by dividing the average second stage (known) head-width by that of the first (known), and the head-width of the penultimate instar by that of its previous exuvium and taking the average.

Average head-width of first instar = 0.75 mm.	} Ratio of increase = 1.33
" " second " = 1.00 mm.	
Head-width of penultimate instar = 8.00 mm.	} Ratio of increase = 1.11
" previous exuvium = 7.00 mm.	
Average head-width = 1.22 mm.	

Calculated head-widths in mm.			Observed head-widths in mm.
Head-width observed in first instar =			0.75
Calculated head-width in second	instar (0.75 × 1.22) =	0.915	1.00
" " third	" (0.915 × 1.22) =	1.116	
" " fourth	" (1.116 × 1.22) =	1.361	
" " fifth	" (1.361 × 1.22) =	1.660	1.5
" " sixth	" (1.660 × 1.22) =	1.915	
" " seventh	" (1.915 × 1.22) =	2.336	
" " eighth	" (2.336 × 1.22) =	2.849	2.75
" " ninth	" (2.849 × 1.22) =	3.475	3.25
" " tenth	" (3.475 × 1.22) =	4.239	4.5
" " eleventh	" (4.239 × 1.22) =	5.171	5-5.5
" " twelfth	" (5.171 × 1.22) =	6.308	6-7
" " thirteenth	" (6.308 × 1.22) =	7.695	7-8
" " fourteenth	" (7.695 × 1.22) =	9.387	8-9

Thus it would seem that the number of instars is exceptionally high; however, the number would be bound to vary with individual larvae, considering their long larval period and how it is influenced by environment.

Pupation.—Throughout past literature, as far back as 1746, there have been conflicting observations regarding the location of the pupal cell of *Prionus*. Early authors state emphatically that the larva pupates in the bole of the tree, near the bark. The following are but a few random examples of this conviction: "... larva forms a large cocoon chiefly composed of chips of wood in which it passes the pupal state; before changing it bores its hole close towards the outer surface of the tree . . ." (Fowler, 1890); "pour construire

cette demeure, elle utilise les matériaux ligneux qui sont autour d'elle" (Planet, 1891); "... pupa enclosed in a large, thick cocoon formed of sawdust or decayed wood" (Curtis, 1838); "... larva makes its way towards the bark of the tree and then forms from the woodchips a cocoon" (Wood, 1876).

On the other hand, Rösel von Rosenhof (1746) figures an earthen cocoon, but merely states that when the larva pupates it requires clay soil to make its cocoon.

In 1889, however, J. C. Bowring observed that several specimens "emerged from roots of oak trees, running along the ground leaving holes like those of bees' nests." A similar observation was recently recorded by Lloyd (1944). Dr. K. G. Blair has recently found pupal chambers of *Prionus* "fairly deep beneath the bark of a fallen birch trunk."

Another controversial point is that concerning the composition of the pupal cell. There are certain records in which it is stated either that the cell consists entirely of wooden chips, or that it is composed of both wood and earth. Box (1915), for example, recounts how he found pupae below a log in cocoons of wooden chips. Cocoons examined by the author in both Surrey and Sussex, however, have always been composed entirely of earth, as are those of certain allied North American species (Craighead, 1915). They were in every case roughly one to three inches below the surface of the soil, and were either constructed against the bole or alongside the underground roots—usually the latter. The cocoon is large and oval, amply accommodating the pupa; it consists of rather fine particles of earth stuck together by a secretion of the larva; the interior is smooth. The external measurements are on an average 45 mm. by 30 mm. It is not possible to include a photograph of one in the present paper, but there is an excellent photograph of a similar cocoon of an allied species in a paper by Craighead (1915).

Edibility of Larva.—Planet (1889) gives an interesting account of the edibility of various larvae, particularly those of *Prionus* and *Cerambyx*. The full-grown larvae, he writes, "ont un aspect tout à fait appetissant, leur peau molle et transparente laissant apercevoir des tissus délicats qui rappellent par leur couleur d'un blanc jaunâtre, les dehors d'une volaille convenablement engraisée." To prepare a larva for consumption, he continues, "salez-la, faites-la mariner un peu, dans du vinaigre, pour rendre la peau moins dure, faites revenir dans du beurre et . . . bon appétit." As a precaution he advises that the larva's head first be removed lest it should cause "un sommeil exotique"!

According to Amoreux, larvae of this species were eaten by the Romans under the name of Cossus.

It is hoped that only a few readers will acquire a taste for this delicacy—lest it should lead to the ultimate extermination of our only British *Prionid*.

Resistance of Larva to Drowning and its Reaction to Low Temperatures.—Despite its size and apparent sturdiness this larva is exceptionally delicate and very susceptible to bruising, a condition from which it will invariably die within hours or days according to the extent.

That it is extraordinarily resistant to drowning is proved by the following experiment. A full-grown larva was immersed in water at 16 deg. C. for a period of 168 hours; after two hours had elapsed it had ceased to engage in regular movements, except when prodded, and had become extremely flaccid, its ampullae no longer being protuberant.

When transferred to dry filter paper it completely revived within fifteen minutes.

Upon repeating the experiment with another larva, the revival period was reduced to one-third merely by immersing the larva in warm water (40 deg. C.). Thus it seemed that the larva's flaccidity was promoted through the low temperature of the water, rather than through the water itself. This was substantiated by a further experiment, in which a larva was placed in a refrigerator and subjected to a temperature of 5 deg. C. for one hour, with the result that it became equally flaccid and inert. It soon became active, however, upon being immersed in warm water, but maintained its flaccidity until allowed to dry off. The same larva was later subjected to -6 deg. C. for 12 hours, and when removed it remained frozen stiff for nearly an hour; it was then placed in an incubator at 40 deg. C., where it revived two hours later.

Many larvae doubtless become submerged in water for days at a time, as roots excavated by them would naturally often become flooded during rainy periods; but this resistance to drowning and frost, as proved in the above experiments, indicates that they are well able to withstand severe weather conditions.

Parasites and Natural Enemies.—In a paper by Elliott and Morley (1907), it is mentioned that *P. coriarius* has been observed to be parasitised by the ichneumon *Xorides albicans* Grav.; this has been substantiated by the present author, who caught several adults⁵ exploring a *Prionus*-infested stump last August. *Molochius minor* L., and *Aromia moschata* L. were also found to be its hosts. As the adult parasites normally occur during July and August, it seems probable that the *Prionus* larvae are parasitised in their first or—at the latest—their second stadium (which is attained in the autumn), for by the following year they would have reached the underground roots or the heart wood, and would thus be safe from attack. A photograph of this parasite is shown on Plate 1.

No dipterous parasites appear to have been recorded. Lucas (1914) describes how on one occasion he gave some *Prionus* eggs to a very large centipede (*Lithobius*), which fed on them readily. Young larvae are probably likewise consumed, and, judging from the abundance of these creatures in many *Prionus*-stumps, it would seem likely that they play an appreciable part in the control of this insect.

On numerous occasions the author has found larvae of *Melanotus rufipes* Herbst (Col., ELATERIDAE) and *Rhagium bifasciatum* F. (Col., CERAMBYCIDAE) in the same wood as *Prionus* larvae; the former is an acknowledged predator on many lignicolous larvae, and *Rhagium* larvae, though not actually predatory, will readily bite any soft-bodied larva that intrudes upon their burrows. Several species of ants have been found from time to time in *Prionus*-stumps, but they do not appear to invade the occupied portions of the burrows; the accumulation of frass and shavings behind the larva would, in any case, present a barrier.

The only reference that could be found regarding natural enemies was that by Champion (1926), who states that he saw a male captured by a small bird (sparrow?) which dropped it alive and tried to recapture it. This was presumably in the daytime. No evidence of woodpeckers attacking *Prionus*-infested stumps is available.

Methods of Preservation.—Compared with the majority of coleopterous larvae, this species is exceptionally difficult to preserve, and several methods have been tried in an attempt to maintain the original form and colour. All attempts to preserve these larvae in the dry state (i.e., by removing the abdominal contents and inflating with hot air) failed, as they turned

⁵ These were identified by Mr. G. E. J. Nixon (British Museum, Natural History).

completely black; this was presumably due to the high fat content of the integument. Those killed and preserved in 70% alcohol invariably shrivelled appreciably and turned brown or dark-grey and the ampullae became depressed, thus depriving the larvae of their natural form. Immersion in Pampel's Fluid (Imms, 1939) for three to six days prior to preserving in alcohol proved to be a more satisfactory method, though there was still a certain amount of discoloration. The most satisfactory procedure was eventually found to be that of placing the larva in a test-tube of weak alcohol (30-50%) to which had been added two or three drops of acetic acid, and heating the tube carefully, maintaining a temperature just below boiling point for ten to twenty minutes, according to the size of the larva, which should then be kept permanently in 70% alcohol.

HABITATS.

As the following records indicate, this larva is more or less polyphagous, and there can be comparatively few common species of our larger trees which have escaped its ravages:—Bedel (1901), oak, beech; Fowler (1890), oak, beech, horse-chestnut, ash, etc.; Planet (1891), oak, and others, especially cherry; Schiödte (1876), oak, beech, horse-chestnut, ash. Various subsequent authors mention birch, elm, hornbeam and plane.

Oak appears to be the first of its food plants to be recorded in this country (e.g., Janson's *British Beetles*, 1863), as well as being the tree most commonly attacked. Records of this larva from pine appeared later, that by Lloyd (1944) being the most recent one. It is unusual for a lignicolous species to attack both deciduous and coniferous trees; moreover, the species seems to have no preference and oviposits on either indiscriminately, for the author recently obtained larvae from both birches and pines which were growing together in the same strip of woodland. It has been the author's experience (at least in Middlesex, Surrey, Hants and Sussex) that oak, birch and beech are the most frequently attacked, though larvae were also taken from pine (on two occasions), willow, and even holly.

Early records are vague and give no indication as to the root-feeding propensities of the species. For example, Curtis (1838) states: "The larvae live in large trees which are in a decayed state"; Bedel (1901) is more explicit, stipulating "au pied des vieux arbres"; and Planet (1891) states: "dans les souches mortes ou dans les troncs pourris ou déjà malades."

During this investigation the author has occasionally found larvae in the heartwood of trees and stumps, but they had never tunnelled for more than a foot above ground level. On two occasions mature larvae were taken from a rotten, punky log (oak?), and a felled tree which had been left to lie on the ground; in both these instances the trees had obviously been felled shortly after the eggs had been deposited, and the larvae, having no roots to explore, were confined therein. Had this timber been lying in a drier situation, the larvae would doubtless have perished before attaining maturity; for these larvae thrive only in moist wood (hence their root-feeding propensities?), and, despite occasional exceptions, they prefer to feed in the underground roots rather than in the bole. It also seems (at least, in the area surveyed) that trees growing in light, even sandy, soil on the edges of woods—especially those in rather damp, though not necessarily flooded, situations—are most prone to attack.

COLLECTING AND REARING METHODS.

As pointed out in a previous paper by the author (1946), this impressive insect is seldom to be taken in large numbers; in fact, if a collector secures a dozen specimens throughout a decade he is fortunate, as it is only in exceptional circumstances that this species is found to be at all abundant. Such instances are few and far between and are usually due to the collector having lived in or near a favourable locality, whereas the majority have only been able to make occasional visits to such terrain.

The beetles may be collected in four different ways: by relying on the chance discovery of specimens at rest on tree trunks, fences, etc., in daylight; by patrolling likely terrain at dusk, net in hand, on the look-out for adults on the wing; by "sugaring" the boles of trees; and by attracting them by means of car headlights, petrol-vapour lamps, etc. The success of the last three methods is governed to a great extent by weather conditions, warm, sultry, August evenings being most favourable.

It is the author's contention, however, that by far the most satisfactory method of obtaining this insect is that of securing a larval colony, because not only does it eventually provide the coleopterist with a series of perfect adults in a comparatively short time, but it also enables him to become acquainted with the transformations and habits of this interesting species.

The collector who wishes to secure larvae must be prepared to spend many hours of often strenuous work, and should be equipped with a trowel, hammer, chisel and saw with which to expose and reduce stumps and roots to sufficiently small pieces to reveal them. It is only occasionally that infested wood is sufficiently rotten not to make work laborious. Trees that have been recently dug up or blown down so that their roots are exposed should be chosen whenever possible, as much time will thus be saved in digging. Two points to bear in mind are: as soon as frass is revealed, proceed slowly and with care, as larvae have a very delicate integument; and always segregate larvae, as they will readily bite one another, often with fatal results. The characteristics of suitable localities and habitats of *Prionus* have already been dealt with elsewhere in this paper (see p. 438).

The most reliable and convenient method of rearing larvae with a view merely to obtaining a series of adults, is to saw off a section of the infested root or stump (the larger the better) and also a similar section of wood which has not been severely attacked, both of which should be transferred to one's garden. Here they should be rested side by side on top of a large, shallow tray filled with light soil or sand. They should then be covered with small-mesh wire netting (the edges of which may be either tacked to the sides of the tray or tucked beneath it) and placed in the dampest, most shady part of the garden, where they should be watered from time to time if necessary. Should the larvae exhaust their food supply before pupating, they will readily bore into the sound section.

For the close observation of individual larvae, a small section of root (roughly 9-12 in. in length, and 3-5 in. in diameter) should be sawn or split in half longitudinally. A groove should then be cut in the inner face of one of the halves, large enough to accommodate the larva. Next place the larva in position and carefully press the two halves of root together, securing them with two small leather straps or wire ligatures. The end containing the larva should then be placed in an earthenware pot filled with light, rather damp soil or sand, so that roughly two-thirds of the log are exposed. If kept indoors, a well-

ventilated, sunless situation should be chosen. Every two or three weeks the pot should be stood in water for a few minutes. The logs should be renewed periodically, and care must be taken to remove all moulds and fungi should they appear. As soon as the larva shows signs of pupating, cover the pot with gauze or place it in a ventilated cage, and stand it in a sunny situation.

ECONOMIC IMPORTANCE.

Dr. R. C. Fisher has informed the author that *Prionus* is not considered a serious timber pest in this country, and that, consequently, no control measures are taken against it. No instances have come to his notice of this species infesting the bole of a standing tree; and this has been substantiated throughout the present investigation (see "Habitats," p. 438) in which larvae were found in nearly every case to be infesting the roots only, the exceptions being those found at the bases of boles.

It is the author's contention that the economic importance of this species is limited by three factors, namely: 1. Although widely distributed, the species is not sufficiently abundant. 2. Adults prefer living, mature, but usually damaged, trees or stumps on which to oviposit. 3. Trees planted for their commercial value are invariably felled before maturity is reached.

The fact still remains, however, that these larvae cause considerable damage to the roots of living deciduous and coniferous trees, and, although their importance with regard to the timber industry may be negligible, the damage caused to ornamental trees in plantations, parklands, and mature woodlands cannot be lightly disregarded.

DISTRIBUTION IN GREAT BRITAIN.

This insect is widely distributed throughout southern England, but is more localised in the Midlands (see fig. 17). No records farther north than Lancashire were to be found. It appears to thrive chiefly in deciduous woodlands (though occasionally in coniferous ones), especially those of long standing.

Epping Forest and the New Forest are the two areas in which it has been observed most abundantly; although this is no doubt due to the maturity and great variety of the local timber, the fact that both these areas have always been popular with entomologists as hunting grounds should not be overlooked. Larval colonies in Surrey, Hampshire, Sussex and Middlesex have recently been found by the author. Ravages of larvae, suspected as being those of *Prionus*, were seen in Wiltshire, but owing to inconclusive evidence this has not been indicated on the map.

There are only two county records for Wales, only one of which is comparatively recent (*i.e.*, 1914). There appears to be no evidence of this species ever having been indigenous in either Scotland or Ireland.

STATUS OF COLONIES.

Owing to its nocturnal habits, it has not been possible to furnish a reliable estimate of the numerical status of *Prionus*. Building operations and—to a far more drastic extent—the wholesale felling of many thousands of our limited supply of mature trees to meet the demands of two national emergencies, will have doubtless appreciably restricted, if not exterminated, a large proportion of colonies throughout the past forty-five years.

This coleopteron has always been reasonably plentiful throughout the

New Forest, and Mr. F. H. Haines in a recent letter to the author states : ". . . it is fairly common in the Forest and here, on my ground, at Linwood and at Gorley." On the other hand, records for Suffolk even in the last century were only very occasional, and no recent records for this county were to be found. According to Fowler, *Prionus* was widely distributed in Norfolk; of recent years it appears to have been commonest in the upper Bere region. There appears to be no recent decline in records from Hampshire, Surrey, and



FIG. 17.—Map showing distribution of *P. coriarius* L., in Great Britain.

Essex, and it is still to be taken fairly abundantly in Herefordshire (Lloyd, 1944).

From personal experience in the field, the author is firmly of the opinion that if collectors were to search for larval colonies, a procedure which, it is hoped, will have been facilitated by information given in this paper, instead of waiting for chance captures of adults, this beetle would prove to be more abundant and widespread than past records indicate.

REFERENCES.

- BEDEL, L., 1901, *Faune des Coléoptères du Bassin de la Seine* 5 : 4.
 BOX, H. E., 1915, *Ent. mon. Mag.* 51 : 310.
 CHAMPION, G. C., 1926, *Ent. mon. Mag.* 62 : 219.

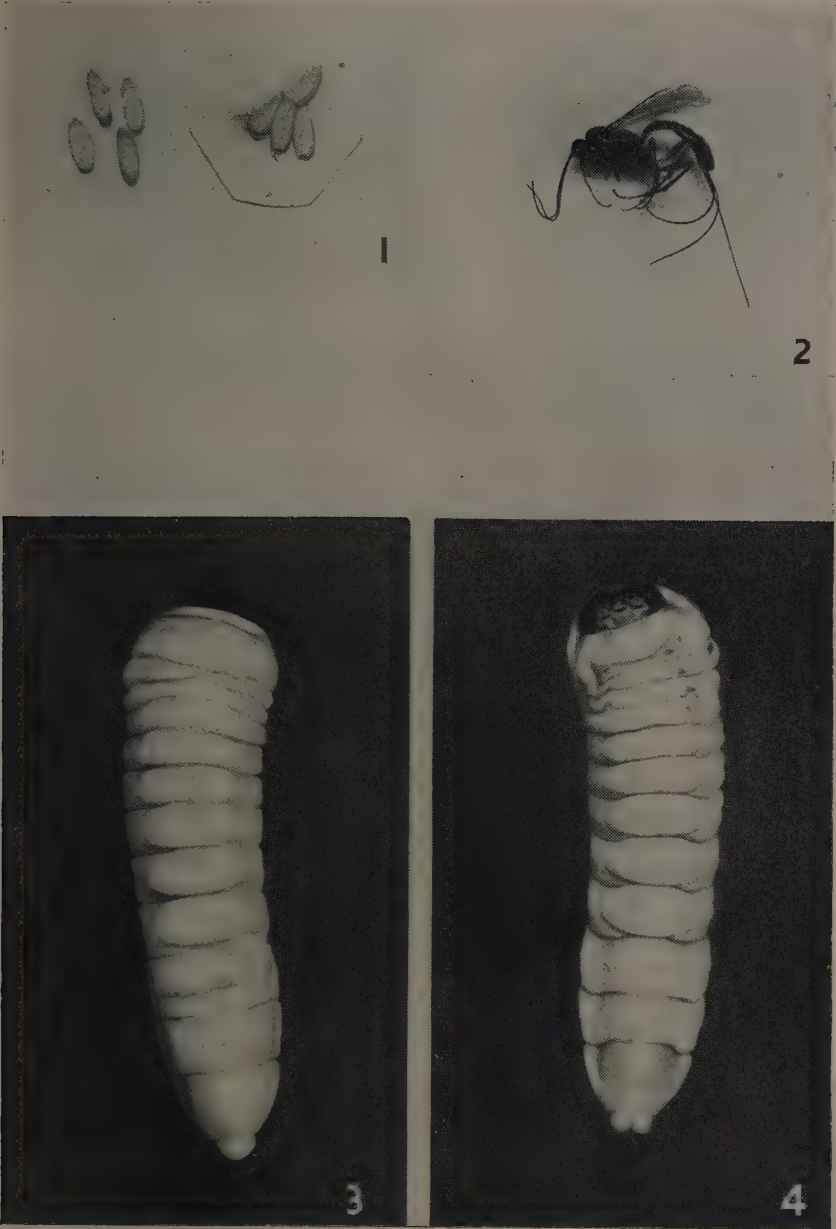
- CRAIGHEAD, F. C., 1915, Larvae of the PRIONINAE. *Rep. U.S. Dep. Agric.* **107** : 1-24.
- , 1923, North American Cerambycid Larvae. *Bull. Dep. Agric. Can.* (N.S.) **27** : 1-29.
- CURTIS, J., 1838, *British Entomology* **15** : fo. 746.
- DUFFY, E. A. J., 1945, Coleoptera of the Hants-Surrey Border. *Ent. mon. Mag.* **81** : 177.
- , 1946, Observations on *Prionus coriarius* L. (Col. CERAMBYCIDAE), with particular regard to collecting methods. *Ent. mon. Mag.* **82** : 136-7.
- ELLIOTT, E. A., and MORLEY, C., 1907, The Hymenopterous Parasites of Coleoptera. *Trans. ent. Soc. Lond.* **1907** : 24.
- EMDEN, F. I. van, 1939, Larvae of British Beetles.—1. A Key to the Genera and most of the Species of British Cerambycid Larvae. *Ent. mon. Mag.* **75** : 258-9.
- FOWLER, W. W., 1890, *Coleoptera of the British Islands* **4** : 218.
- HUNT, H. E., 1914, *Entomologist* **47** : 104.
- IMMS, A. D., 1939, A "safe" fluid for museum use. *Nature* **144** : 599-600.
- JOY, N. H., 1932, *A Practical Handbook of British Beetles* **1** : 374.
- KRAUSE, A., 1888, *S.B. Ges. naturf. Fr. Berl.* **1888** : 145.
- LAMEERE, A., 1885, Contributions à l'histoire des metamorphoses des Longicornes de la Famille des PRIONIDAE. *Mém. Soc. Sci. Liège* **11** (11) : 16.
- LLOYD, R. W., 1944, *Ent. mon. Mag.* **80** : 248.
- LUCAS, W. J., 1914, *Entomologist* **47** : 252.
- MARIÉ, M. P., 1924, *Bull. Soc. ent. France* **1924** : 80.
- PINHEY, E. C., 1936, *Proc. S. Lond. ent. nat. Hist. Soc.* **1935-36** : 32.
- PLANET, L., 1889, Larves comestibles de Coléoptères. *Naturaliste* (2) **3** : 280.
- , 1891, La Larve et la Nymphe du Prion Tanneur. *Naturaliste* (2) **5** : 31.
- REITTER, E., 1912, *Fauna Germanica, Käfer* **4** : 3.
- RÖSEL VON ROSENHOF, A. J., 1746, *Der Insekten-Belustigung*. **2** : 15-20.
- SCHIÖDTE, J. C., 1863, Danmarks Cerambyces. Transl. in *Ann. Mag. nat. Hist.* (3) **15** : 182-209.
- , 1876, De Metamorphosi Eleutheratorum Observationes. *Naturhist. Tidsskr.* (3) **10** : 369-458.
- SCHNEIDER, W., 1884, *Z. Ent.* (2) **9** : xx.
- WOOD, J. G., 1876, *Insects at Home*.

PLATE 1.

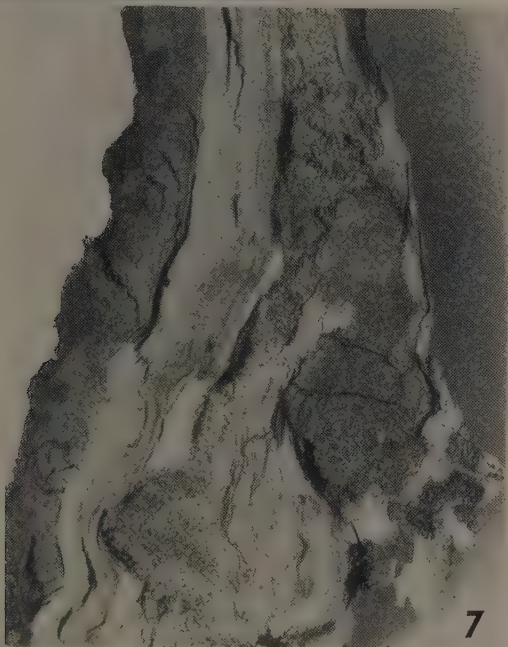
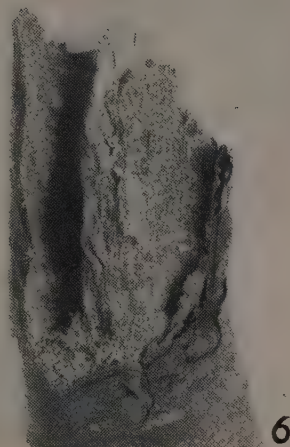
- FIG. 1. Eggs of *Prionus coriarius* L. ($\times 2$); the group on the right have hatched.
2. Adult of *Xorides albicans* Grav. ($\times 1\frac{1}{2}$), a parasite of *Prionus coriarius* L.
3. Full-grown larva of *Prionus coriarius* L., dorsal aspect (life size).
4. Full-grown larva of *Prionus coriarius* L., ventral aspect (life size).

PLATE 2.

- FIG. 5. Cross-section of larval gallery ($\times 1$).
6. Section of root exhibiting damage by a *Prionus* larva ($\times 1$); the thin covering of bark and the hard central core are all that remain.
7. Section of a birch stump showing larval galleries tightly packed with coarse frass ($\times 1$).



E. A. J. Duffy. Biology of *Prionus coriarius* L.



E. A. J. Duffy. Biology of *Prionus coriarius* L.

Vol. 97. Part 18. Pp. 443-472, 7 figs.

29th November, 1946.

THE

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

X FRASER, Lt.-Col. F. C., I.M.S. Retd., F.R.E.S.

Notes on Amazonian Odonata in the Leeds

Museum

443-472, 7 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 10s.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

J. W. EVANS, M.A., D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. British National Committee for Biology (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. Local Committee of Management of Wicken Fen.

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. National Trust for Places of Historic Interest or Natural Beauty.

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. New Forest Association.

Mr. W. Fassnidge, appointed 1934.

5. New Forest Joint Committee.

Mr. W. Fassnidge, appointed 1939. Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. Royal Meteorological Society. Phenological Committee.

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. Council for the Promotion of Field Studies.

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

8. Joint Bioclimatic Committee.

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

NOTES ON AMAZONIAN ODONATA IN THE LEEDS MUSEUM

By Lt.-Col. F. C. FRASER, I.M.S. Retd., F.R.E.S.

Manuscript received 25th March, 1946.

(Read 2nd October, 1946.)

WITH SEVEN TEXT-FIGURES.

(Continuation and conclusion.)

THE first part of this paper dealing with the rich collection of Odonata from Peru and Colombia in the Leeds Museum appeared in these *Transactions* (96 : 11-46, 1946); in this second and final paper, the remainder of the Zygoptera and the whole of the Anisoptera are dealt with. The topography of the habitats, in Colombia and Peru in which the species were collected, is similar to that outlined in the preface to the first paper and need not be repeated here : the reader is referred to it for further information, but will find individual habitats mentioned under each species in the present paper. At the end of the present paper, the bibliography involved in the two papers is given in chronological order.

Eleven new species are described here, mainly belonging to the genus *Argia* Selys. One of these, however, a new *Microstigma*, has been included here for convenience and actually comes from Bolivia; it was pronounced as new by Dr. Erich Schmidt some two years before the war and the type has been in my collection since 1934. The description of other species belonging to the family PSEUDOSTIGMATIDAE in the Leeds Museum collection has offered a favourable opportunity for describing it.

Zygoptera (cont.).

Heliocharis libera Selys.

A single pair from S.E. COLOMBIA : Upper Putumayo River, 24.vii.30.

These do not differ from type or from males in my own collection from Porto Velho, Brazil. There are some differences in the minor details of venation but these are invariably present in annectant forms such as this genus represents. Selys, in 1869, united the genera *Dictierias* Selys and *Heliocharis* Selys because of the discovery of *H. libera* Selys, a species in which the median space was found to be free of cross-veins, thus differing from the genotype in which the same space has 4 traversing veins. He re-established *Heliocharis* as a subgenus of *Dictierias*, giving as the principal character for differentiation the origin of the median sector (Riv + v) distal to the level of the discoidal cell, and this same sector not contiguous with the median vein (Ri). I have already pointed out that the amount of recession of the origins of the principal veins and lengthening of the intercalaries is the surest method for estimating the progress of evolution among the genera and species. In some of the Agrioidea, this recession and lengthening respectively has gone on to such a degree that a point has been reached where it can proceed no farther without an actual

bowing or buckling of the veins, the result of which has been to arch them forwards until they finally come into contact and fuse with the Radius. In *Heliocharis* such a state has not been quite attained and IRiii is still separated from Ri, and cross-veins can be seen at this level passing between them. In *Dictierias*, however, lengthening and recession has gone on to a greater degree, so that their proximal ends are now nearer the base of wing than in *Heliocharis*, and the buckling of the veins is so great that they have come into contact with and fused with the Radius. Undoubtedly, then, evolution has advanced farther in *Dictierias* than in *Heliocharis*, and the two genera should be considered as still distinct. The two present specimens are rather teneral and the colours and markings are still indistinct: the sides of the thorax are bluish and contrast strongly with the dark submetallic dorsum, the abdomen also shows traces of a pale bluish coloration. In some respects *Heliocharis* resembles the Old World genus *Philoganga* Kirby but this is due to convergence rather than actual close relationship; since the arculus in the former lies remarkably near the basal primary antenodal, whereas in *Philoganga* it lies equally remarkably distal to the distal primary antenodal: the latter genus is far older than the former.

COENAGRIIDAE.

Genus *Argia* Selys.

There is no more difficult genus than *Argia* Selys in the whole Order Odonata; this is partly due to the large number of species, viz. 112, which have been described, and partly due to their homogeneous characters. The black colour with blue markings is, with few exceptions, common to the whole genus and offers few points for differentiation; the genitalia are equally barren in this respect. The character of the pterostigma I find important, whether as long as broad and diamond-shaped or elongate, much longer than broad and narrow. The shape and relative length of the anal appendages, however, is the most reliable and practical character by which the numerous species may be separated one from another. The superiors may be shorter or longer than the inferiors or they may be of equal length; the apical spine of the superior appendages, which is rarely absent, may be evident or concealed when the appendage is viewed in profile but otherwise these appendages are of very similar shape and size in the species. The inferiors offer a much wider range, and a typical one may be said to consist of a broad triangular shape as viewed in profile, with the apex directed upwards and backwards, entire or more often broadly bifid. I am inclined to consider the lower of the two bifurcations as the original apex of the appendage and the upper one as a secondary development. Often the two conical, spine-like bifurcations are well developed, but more often one appears to be developed at the expense of the other, so that with this interplay, it will be seen that a very wide system of variations has been evolved by which the species may be differentiated.

Other factors operate to increase the difficulties of this genus: the difficulties of examining types which are scattered widely in numerous collections and few accessible to the ordinary student, the poverty of the old descriptions, many of which did not contain any account of the anal appendages, and lastly the need for good text-figures of these appendages. A simple outline is the most that has been given by any author, and this I am of opinion is quite inadequate, since it is obvious that the slightest alteration in the angle of view or the normal position of the appendage will greatly alter the shape of that outline. Whilst this would not carry much weight in a small genus, it is of great importance in a

larger one, where differences are often so slight as to be difficult to appreciate unless the greatest accuracy be observed. For the Central South American species of the genus, Calvert's keys and descriptions in the *Biologia Centrali Americana* have been found very useful. A great need exists for a full monograph of the genus. Mrs. Gloyd, who began such a work nearly ten years ago, has been unable to carry it out and now writes to inform me that she has not done any work on the genus for over two years.

In the Leeds Museum collection there are over a hundred specimens of *Argia*, most of which I have been unable to place and which appear to me to be new. Both Förster and Navás have described new species from Peru and Colombia, but I have been unable to fit the present specimens into any of their descriptions.

Argia cuprea Hagen, 1861 (fig. 1, f and g).

Agriion cupreum Hagen, 1861, *Neur. N. Amer.* : 96.

Argia cuprea Selys, 1865, *Bull. Acad. Belg.* (2) 20 : 407.

Argia cuprea Kirby, 1890, *Cat. Odon.* : 138.

Argia cuprea Calvert, 1865, *Proc. Calif. Acad. Sci.* (2) 4 : 479.

Argia cuprea Calvert, 1902, *Biol. Cent. Amer. Neur.* : 71, 73, 84, pl. 4, ff. 22, 41, 41s.

Argia cuprea Calvert, 1902, *Bull. Mus. comp. Zool.* 39 : 108, pl. 1, f. 8, 8a.

Argia cupraurea Calvert, 1902, *Biol. Cent. Amer.* : 71, 73, 85, pl. 4, ff. 24, 42.

Argia cupraurea Calvert, 1902, *Bull. Mus. comp. Zool.* 39 : 107.

Argia cuprea Calvert, 1907, *Biol. Cent. Amer. Neur. Suppl.* : 371.

Argia cupraurea Calvert, 1907, *Ibid. Suppl.* : 371.

Argia cupraurea Calvert, 1909, *Ann. Carnegie Mus.* 6 : 120.

Argia cuprea Muttkowski, 1910, *Bull. publ. Mus. Milwaukee* 131 : 46.

Argia cuprea forma *a* and *b* Ris, 1918, *Arch. Naturgesch.* 82, A, 9 : 110, ff. 56, 57.

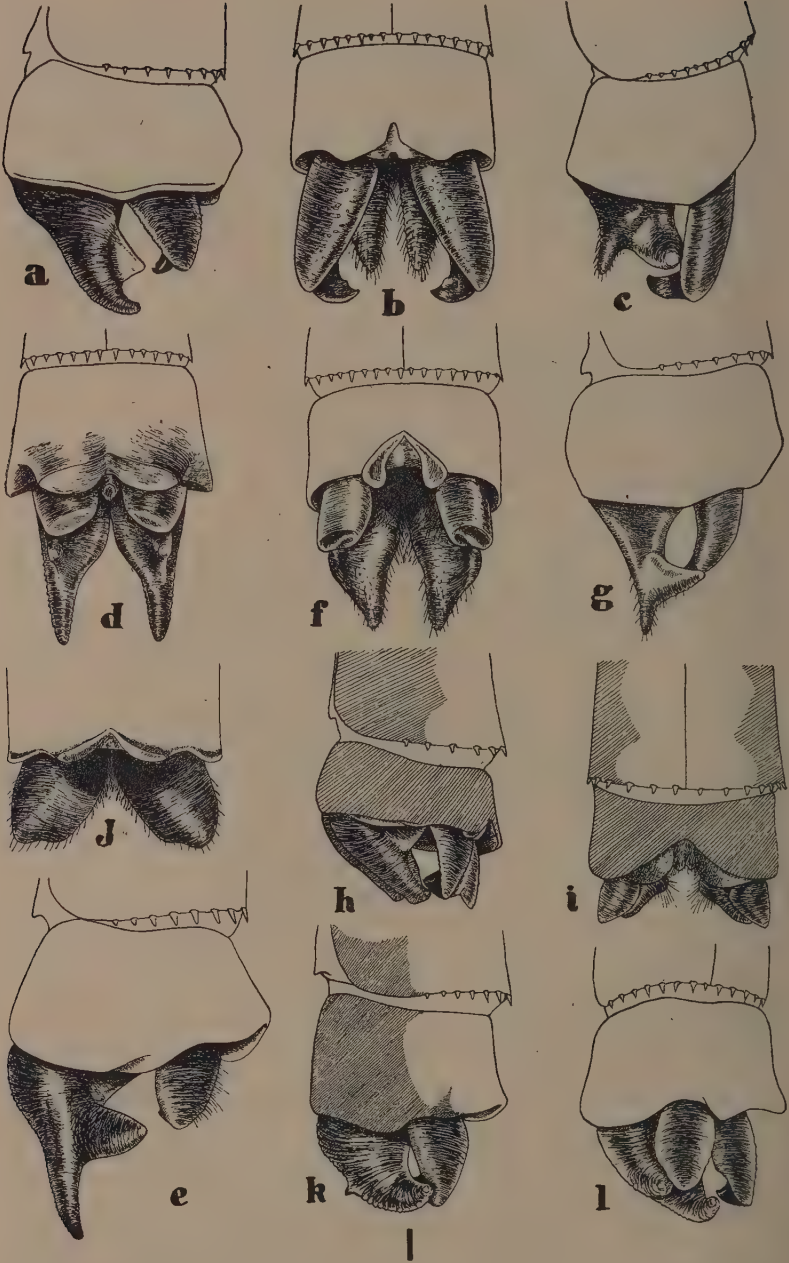
Argia cupraurea Ris, 1918, *Ibid.* 82, A, 9 : 111.

Argia cuprea forma *a* Calvert, 1919, *Ent. News* 30 : 164.

Forma *c* nov. (fig. 1, f and g).

Male. Abdomen 34 mm. Hind-wing 24 mm.

Head : labium pale straw yellow, labrum yellowish, its basal half brilliant coppery metallic, anteclypeus yellow, postclypeus, frons, vertex and occiput brilliant coppery metallic with comparatively small rounded blue postocular spots. Eyes rather broadly bordered with pale creamy yellow below. Prothorax and thorax coppery metallic on dorsum, the former with a small pale area on the lower part of middle lobe and with its posterior lobe broadly rounded. The metallic colouring on thorax extending as far lateral as the first suture, a very small pale bluish spot at upper end of humeral suture, the rest of sides and beneath pale bluish, clouded with ferruginous along the line of the postero-lateral suture, at the upper end of which is a small but well-defined spot of dark reddish-brown. Beneath pulverulent. Legs : coxae and trochanters pale ferruginous, as well as the extreme base of the anterior femora, these last black on extensor and outer surfaces, pulverulent on flexor surface; tibiae black on flexor surface, pale blue on extensor surface, tarsi and claws black. Wings hyaline, not enfumed, 15 postnodals in fore-wings, 13 in the hind-wings, 5 postquadrilateral cells in fore-wings. Pterostigma very oblique, nearly twice as long as broad, covering $1-1\frac{1}{2}$ cells, black with a pale yellow frame and thick bordering nervures; pterostigma of hind-wing more acute distally than that of fore-wing. Abdomen blue marked with black as follows : segment 1 blue with its apical border narrowly glossy reddish-brown, segment 2 with a sinuous narrow black stripe on each side, extending from apical border nearly to base, where it just meets a broader stripe which extends from base and tapers to just short of apical border, running parallel with and just superior to the first stripe. The apices of the last two stripes almost confluent with a short subapical transverse black stripe; segments 3 and 4 with narrow apical rings broadly interrupted on dorsum and sending off a short subapical branch dorsad to nearly enclose a small blue



apical spot; laterally each apical ring sends off a narrow ventro-lateral stripe which extends almost to the base of segments; segments 5 and 6 with the apical black rings broader and complete over dorsum, segment 7 entirely black, 8 black with a small subdorsal subapical blue spot, 9 and 10 broadly azure blue, but black laterally. Anal appendages black. (For shape of these, see fig. 1, f and g.)

Female. Abdomen 31 mm. Hind-wing 24 mm.

Head differs from the male by the presence of a very broad pale blue transverse stripe on frons extending to level of bases of antennae and downwards to involve the genae and bases of mandibles; the metallic parts are dully so, both here and on the prothorax and thorax, which latter is marked by a very broad humeral blue stripe, which overlaps the suture above and encloses a small black spot at upper end of suture. Wings similar but venation rather closer, 16-17 postnodals in fore-wings, 14 in the hind-wings, 4-5 post-quadrilateral cells; pterostigma similar. Abdomen with the black markings much more extensive, the lateral stripes very thick and extending so far on to dorsum of segments that they enclose narrow blue carinal stripes extending from base of segments almost to the apices; on segment 7 this blue stripe becomes linear but again broadens on the dorsum of segments 8 to 10. Anal appendages shortly conical, yellow. Vulvar scales robust, extending to end of abdomen, yellow.

Habitat: PERU: San Antonio. A single pair, type and allotype, which will be deposited in the British Museum (Natural History). The following diagram shows the relationships between the four known forms of *cuprea*.

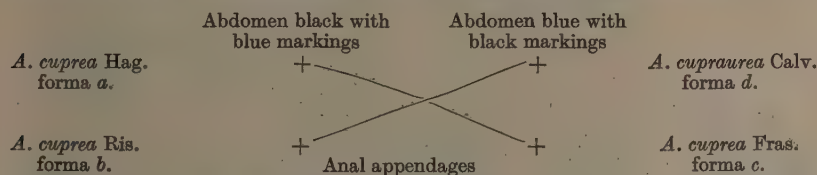


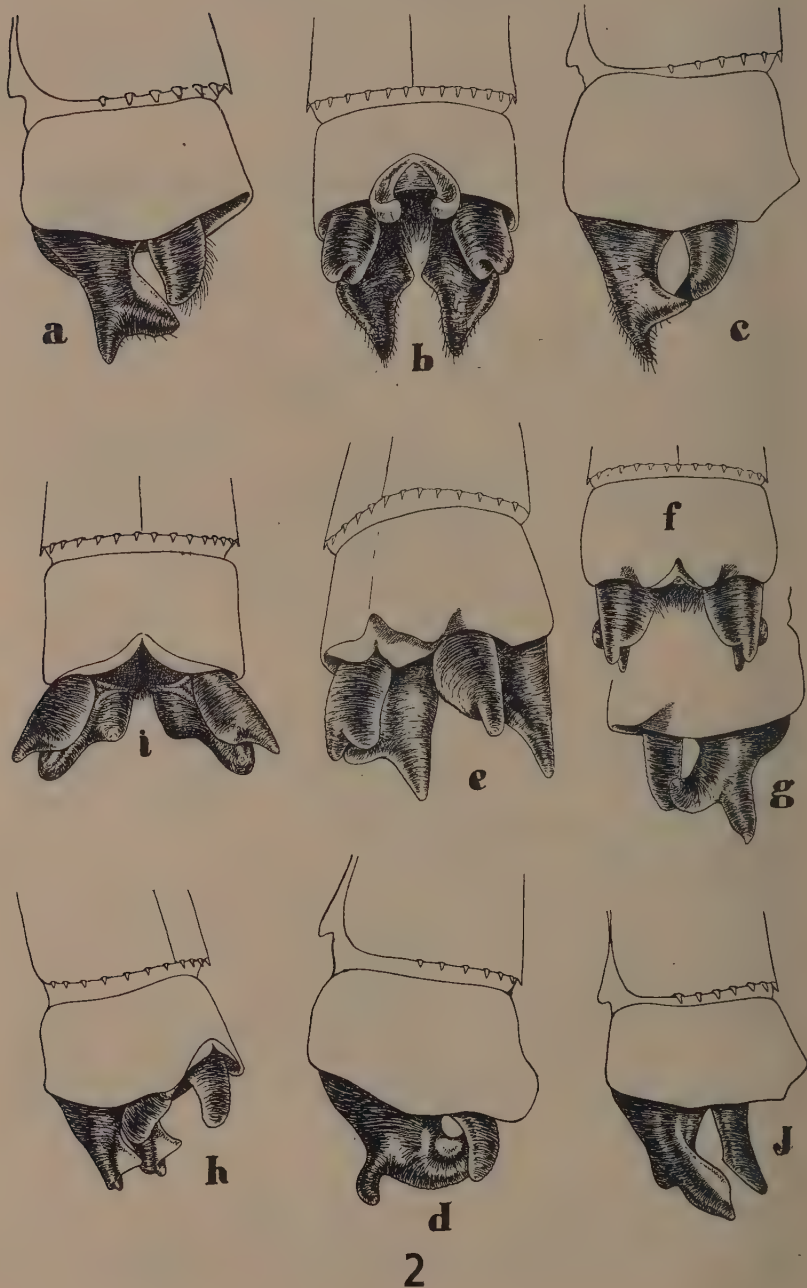
Diagram demonstrating relationship between the four forms of *Argia cuprea* Hagen. Anal appendages of *a* agree with those of *c*, and those of *b* with *d*.

Argia hamulata sp. n. (fig. 2, d).

Male. Abdomen 29 mm. Hind-wing 20 mm.

Head: labium, labrum and whole of head velvety black save for a pair of large azure blue postocular spots; beneath head entirely black. Prothorax black with large paired blue dorsal spots on middle lobe only. Thorax pale azure blue, middorsum black marked with pale blue antehumeral stripes, moderately narrow above but broadening somewhat below where they curl slightly inwards and are slightly narrower than the black bordering them outwardly. Laterally a moderately broad oblique black stripe on the second lateral suture. Beneath thorax pulverulent white. Legs black, coxae and trochanters pale yellow. Wings evenly and rather deeply tinted with brown; 18 postnodals to fore-wings, 15 in the hind-wings; pterostigma elongate, covering one and a half cells, oblique at both ends, brownish-black in colour. Abdomen black, segment 1 with a small triangular blue

FIG. 1.—Male anal appendages of: a. *Argia makoka* sp. n., left lateral view. b. *Argia mishuyaca* sp. n., dorsal view. c. The same, left lateral view. d. *Argia extranea forficula* subsp. n., dorsal view. e. The same, left lateral view. f. *Argia cuprea* forma c, nov., dorsal view. g. The same, left lateral view. h. *Argia trifoliata* sp. n., left lateral view. i. The same, dorsal view. j. *Argia mollusca* sp. n., dorsal view. k. The same, left lateral view. l. The same, left latero-dorsal view.



dorsal spot with its base applied to apical border of segment; segment 2 with a pyriform blue dorsal spot covering the basal three-fourths and tapering to a point apically; segment 3 with a basal dorsal spot tapering rapidly and ending before the middle of segment; segments 4 to 7 black, unmarked; segments 8 and 9 broadly blue on dorsum, this marking narrowing apically on the latter segment; 10 all black. Anal appendages black, slightly shorter than segment 10, of approximately equal length; superiors of the conventional *Argia* form, the apical spine not visible from the side; inferiors trigger-shaped, the short apical portion abruptly narrowed and curled rather strongly upwards and on itself, the dorsal spine enormously hypertrophied and likewise curled strongly on itself and enclosing a short dorsal keel.

Habitat: PERU: Yumbatos, -xi.32. A single male, the *type*. This is a very melanotic species, probably belonging to the *extranea* group, which it most closely resembles, but is distinguished by the shape of its anal appendages.

***Argia trifoliata* sp. n. (fig. 1, h and i).**

Male. Abdomen 26 mm. Hind-wing 20 mm.

Head: labium and labrum black, the latter blue at extreme base, clypeus, frons and genae blue, the rest of head black marked posteriorly with large subquadrate blue postocular spots and a fine brown line on either side the ocellar space diverging forwards. Beneath head black. Prothorax black on dorsum, the anterior lobe, a large rounded subdorsal spot on each side of middle lobe and an oval spot on each side of the posterior lobe azure blue. Thorax black on mid-dorsum and humeral region marked by moderately broad azure blue antehumeral stripes and a small triangular spot at the upper part of the humeral black (Calvert describes this latter marking as a bifurcation of the upper part of the humeral black stripe). Laterally and beneath blue with a moderately broad black stripe bordering the second lateral suture anteriorly but incomplete below. Legs black, the hind femora yellowish internally near the proximal ends. Wings hyaline, untinted, 13 postnodals to fore-wings, 11 to 12 in the hind-wings; pterostigma small, short, covering only 1 cell, broadening slightly distally, this border distinctly rounded, inner border oblique. Abdomen black marked with dark azure blue as follows:—segment 1 laterally and along apical border; segment 2 entirely blue save for a narrow subdorsal black stripe on each side which falls short of both ends of segment but at the apical end is strongly angulated over the dorsum to become nearly confluent with the stripe on the opposite side; segments 3 to 6 each with a broad stripe falling just short of the apical ends of segments; 7 entirely black; 8 to 10 blue on dorsum but encroached upon laterally by black so that on segment 9 the blue is shaped like a trefoil leaf and on segment 10 is restricted to its basal half. This latter segment broadly and deeply bifid at apex. Anal appendages black, of approximately the same length and nearly as long as segment 10; superiors of the conventional *Argia* shape with the apical spine easily visible from the side: seen from above, conical, from the latero-dorsal aspect, deeply and broadly bifid; inferiors sloping very obliquely upwards, broad at base, tapering to an obtuse truncated apex, the dorsal spine fused with apex, almost obsolete and only a vestigial keel present.

Female. Abdomen 26 mm. Hind-wing 20 mm.

Head: labium pale brown, labrum greenish-yellow, postclypeus black, rest of head

FIG. 2.—Male anal appendages of: a. *Argia huallaga* sp. n., left lateral view. b. *Argia cuprea* Hagen, dorsal view. c. The same, left lateral view. d. *Argia hamulata* sp. n., left lateral view. e. *Argia extranea euphorbia* subsp. n., right latero-dorsal view. f. The same, dorsal view. g. The same, right lateral view. h. *Argia infrequentula* sp. n., left latero-dorsal view. i. *Argia umbriaca* sp. n., dorsal view. j. The same, left lateral view.

similar to the male but a broad greenish-yellow fascia bordering the underside of the eyes. Prothorax and thorax similar to the male; legs black but all femora broadly yellow on outer and flexor surfaces proximally. Wings hyaline, untinted, 12 to 13 postnodals to fore-wings, 10 to 11 in the hind-wings; pterostigma blackish-brown, of similar shape and size to the male. Abdomen black, marked sparingly with greenish-blue, a sinuous elongate spot on the sides of segment 1, a broad stripe on each side of segment 2 tapering apically or actually interrupted apically and then shaped like an exclamation mark; segments 3 to 6 with narrow lateral stripe restricted to the middle two-fourths of each segment and tapering to a point basalwards, each of these segments also with a basal ring; segment 7 unmarked; segments 8 and 9 marked with blue dorsally, 8 entirely so on dorsum and subdorsally but, in some, with the base narrowly black; segment 9 with the blue restricted to the apical half of segment, where it is shaped as in the male, trifoliately; segment 10 unmarked. Anal appendages as long as segment 10, conical, black. Ovipositor robust, extending to end of abdomen.

Habitat: S.E. COLOMBIA: Umbria, 30.xi.30, 27.xii.30, 6 males and 2 females. This species is distinguished from others by the shape of the anal appendages without dorsal spine and keel to the inferiors and by the trefoil-shaped blue markings of segments 8 and 9.

***Argia huallaga* sp. n. (fig. 2, a).**

Male. Abdomen 28.5 mm. Hind-wing 20 mm.

Head: labium black, white at extreme base: labrum, clypeus, genae and anterior part of frons dark azure blue, rest of head black with the usual rather large subtriangular post-ocular blue spots. Beneath head dull black. Prothorax velvety black marked with dark azure blue as follows: the anterior lobe, a large rounded subdorsal spot on each side of the middle lobe, a broad fascia on each side of this same lobe narrowly interrupted anteriorly, finally the extreme outer ends of the posterior lobe. Thorax broadly velvety black on dorsum with narrow antehumeral dark azure blue stripes which are much narrower than the bordering black posteriorly. Laterally blue with a rather broad black stripe on the second lateral suture. Legs black. Wings palely tinted with brown, pterostigma very narrow and elongate, covering 2 cells, blackish-brown: 15 postnodals to fore-wings, 13 in the hind-wings. Abdomen black marked with royal blue as follows:—segment 1 entirely save for a small basal dorsal quadrate spot; segment 2 with the lower parts of sides, a broad elongate rectangular middorsal spot which is narrowly separated from a preapical rounded spot (this blue spot is formed by a confluence apically of the broad subdorsal black stripes); segments 3 to 6 with basal middorsal stripes, broad at base of segments but tapering rapidly apicad and decreasing in length gradually from segment to segment, covering the basal half of segment 3 and about the basal fifth and sixth of 5 and 6. Segment 7 entirely black; segments 8 to 10 broadly blue on dorsum, this blue area tapering apicad on segment 8, which also has a small apico-lateral blue spot. Anal appendages black: superiors two-thirds the length of segment 10, of the conventional *Argia* shape, the apical spine not visible in profile; inferiors as long as segment 10, apex directed straight backwards, the dorsal spine slightly longer than apex, robust, with a keel extending from apex to base. In profile this appendage appears to be strongly and deeply bifid on account of the subequal apex and dorsal spine.

Female. Abdomen 28 mm. Hind-wing 22 mm.

Very similar to the male but more robust, the wings evenly and distinctly tinted with brown. Labrum and base of clypeus black, the paler parts olivaceous except for the exceptionally large postocular spots. The outer spot on posterior lobe of prothorax larger. Pterostigma of the same size as male but rather more acute at both ends and paler in colour; 14 postnodals to fore-wings, 13 in the hind-wings. Legs black, femora on flexor surfaces

and tibiae on extensor surfaces pale yellow, especially on the latter. Abdomen black, more sparingly marked with blue, the dorsal spots on segment 2 much smaller and more widely separated, dorsal markings on segment 3 confined to rather less than the basal half, on segment 4 to the basal third and on 5 and 6 mere small basal triangles; segments 8 and 9 with crown-shaped apical azure blue dorsal markings extending nearly to base of 8 but restricted to the apical half of 9: segment 10 entirely blue on dorsum. Anal appendages black, shortly conical. Ovipositor robust and extending beyond the end of abdomen.

Habitat: PERU: Yumbatos, Huallaga region, x.32. Two males and a female. This species resembles in its colouring Förster's *Argia variegata* from the same region, but I am unable to reconcile the anal appendages with his description; they appear to be very different.

***Argia umbriaca* sp. n. (fig. 2, i and j).**

Male. Abdomen 22 mm. Hind-wing 16 mm.

Head: labium brown, labrum blue with base narrowly black, clypeus, genae and anterior part of frons blue as also the large rounded postocular spots, rest of head, including lower surface, black. Prothorax blue laterally, black on dorsum marked with two very large subdorsal blue spots on middle lobe and small spots on outer ends of posterior lobe. Thorax broadly black on dorsum, blue laterally; narrow, slightly curved blue antehumeral stripes, which are narrower than the black area bordering them outwardly. A dark warm-brown stripe over the whole length of the second lateral suture; beneath pulverulent white. Legs entirely black. Wings evenly tinted with brown, often deeply so, 16 to 17 postnodals in fore-wings, 13 to 14 in the hind-wings. Pterostigma elongate, covering one and a half cells, oblique at both ends, dark brown. Abdomen black, segment 1 with a pair of dorso-apical blue spots and the sides blue; segment 2 with a large longitudinally oval violaceous-blue spot confined to the basal two-thirds of segment; vestiges of basal blue rings on segments 3 and 4; segment 9 with the whole of dorsum blue; 10 unmarked. Anal appendages black, divaricate; superiors as long as segment 10, narrow and cylindrical and with the apical spine visible in profile, broadly and shallowly bifid at apex as seen from the dorsum. Inferiors about one-third longer, apex very obtuse and shortened, the dorsal spine much longer, curling evenly dorsad and with a well-developed dorsal keel.

Female. Abdomen 20 mm. Hind-wing 17 mm.

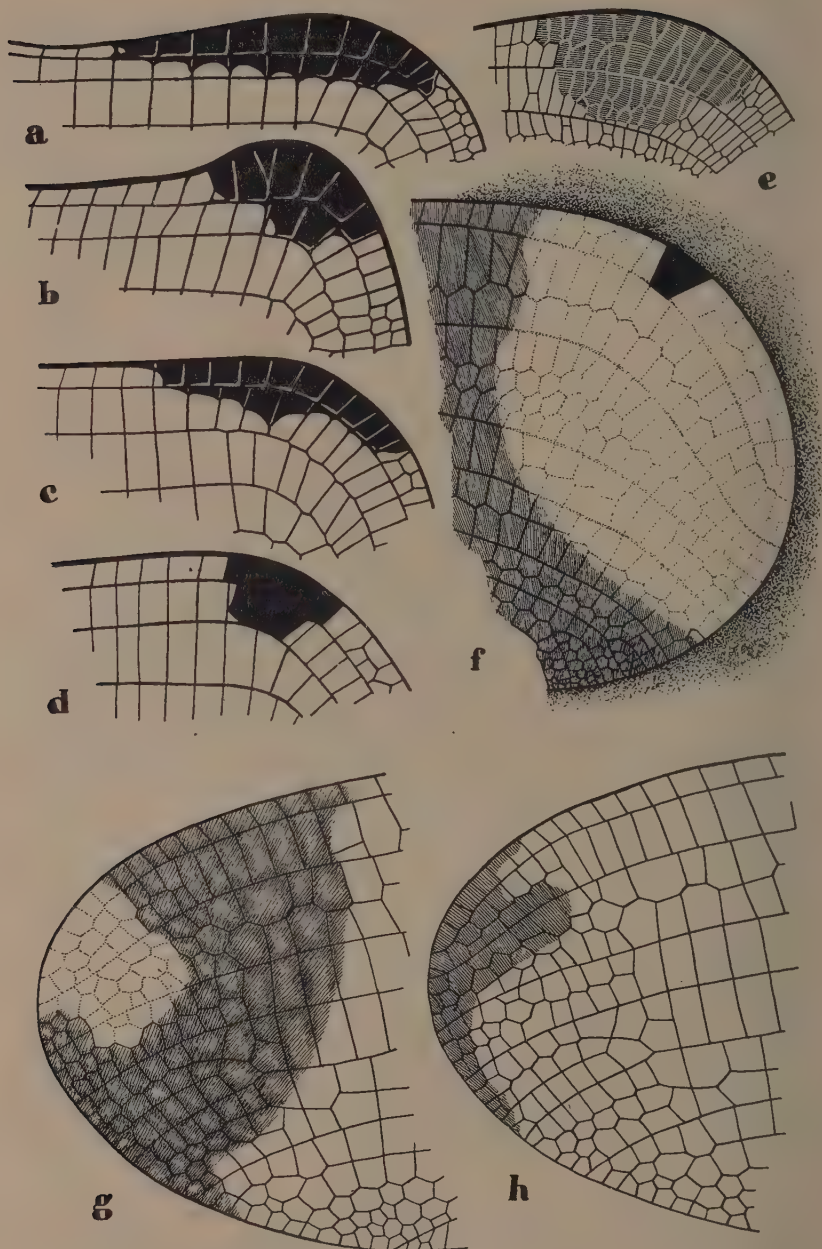
Very similar to the male, differs in the following particulars:—wings more deeply tinted brown; pterostigma rather longer and with the distal and posterior sides in a continuous convexity; 14 postnodals to fore-wings, 12 to 13 in the hind-wings. Postclypeus with its base and a prolongation on both sides black. Segment 1 of abdomen with the blue on dorsum and sides confluent; segment 2 with only a trace of blue on the sides; segments 3 to 7 immaculate; 8 with a dorso-apical blue band covering one-third of the segment; 9 with a 3-pointed crown-shaped spot on its apical half. Anal appendages black, shortly conical; ovipositor slightly overlapping the end of abdomen.

Habitat: COLOMBIA: Umbria, 28.xi.30, 3 males and a single female. This species is distinguished from others by the characteristic formation of its anal appendages and the close venation of its wings, as evidenced by the high nodal index.

***Argia infrequentula* sp. n. (fig. 2, h, fig. 7, d).**

Male. Abdomen 24 mm. Hind-wing 18 mm.

Head (subteneral condition; the markings, in the full adult, largely obscured by melanism): labium whitish, labrum, clypeus, genae and frons blue, postclypeus black or pale; rest of head black except for the large blue postocular spots which in tenerals are



broadly connected by a transverse band of the same colour. Beneath head black, but the eyes narrowly bordered here with yellowish. Prothorax black, the sides broadly, the anterior lobe on dorsum, two median closely apposed triangular spots and very large subdorsal spots on the middle lobe, as well as the outer ends of the posterior lobe azure blue. Thorax blue laterally, broadly black on dorsum and humeral regions, enclosing on the former rather narrow antehumeral blue stripes. The humeral black broader than the antehumeral stripes and bifid above where it encloses a small triangular blue spot. A moderately broad black stripe over the second lateral suture; pulverulent white in adults beneath thorax. Legs black in adults but creamy yellow on the flexor surface of femora and extensor surface of tibiae. Wings hyaline, uncoloured; pterostigma small, quadrate, both ends oblique, covering one cell, dark brown; 16 postnodals in fore-wings, 14 in the hind-wings. Abdomen black, segment 1 bordered apically and with its sides blue; segment 2 with a conical-shaped dorsal blue spot on its basal two-thirds, tapering apicad; segments 3 and 4 with small dorsal basal triangular blue spots; segments 5 to 7 immaculate; 8 to 10 broadly blue on dorsum. Anal appendages black, short, approximately equal in length and a little shorter than segment 10, which is broadly and deeply notched at its apical border. Superiors of the conventional *Argia* shape, the apical spine not visible in profile. Inferiors truncate, emarginate as seen from the side, apex and dorsal spine confluent broadly, the latter slightly overlapping the former and with a large conspicuous triangular keel.

Female. Abdomen 22 mm. Hind-wing 19 mm.

Very similar to the male, especially to the teneral state of the latter. The basal spots on segments 3 repeated on 4 to 7 but vestigial in the latter. Segments 8 and 9 broadly blue on dorsum. In the adult female, as in the male, the blue markings tend to become largely obscured and those on the abdomen entirely lost save on the end segments. The wings hyaline, untinted with brown. Anal appendages black, shortly conical. Ovipositor extending beyond end of abdomen.

Habitat: COLOMBIA: Umbria, 12-23.xi.30, several males and females. This species is closely related to *A. pulla* Hagen by the shape of its appendages and through it to *frequentula* Calvert and *gaumeri* Calvert. The appendages differ, however, by the very large dorsal keel and equally abbreviated apex of inferior appendages. Calvert remarks that considerable variation exists in the shape of these structures, but I am inclined to regard these differences as specific rather than variations. When it is recognised that any difference in their shape must be compensated by a complementary difference in the shape of the prothorax of the female, the significance of this character will be appreciated. Förster's *A. dagnina* may be synonymous, but I am unable to reconcile his description of the appendages of the former with this new species.

Argia mishuyaca sp. n. (fig. 1, b and c).

Male. Abdomen 26 mm. Hind-wing 17-18 mm.

Head coal black save for a small squarish spot against each eye opposite the insertions of the antennae, and large rounded postocular spots which are azure blue. Below the eyes are bordered narrowly with pale blue or yellow. Prothorax black, the lower parts of sides

FIG. 3.—Pterostigma of: a. *Mecistogaster marchali hauxwelli* Selys, ♂, hind-wing. b. *Mecistogaster lucretia* (Drury), ♂, hind-wing. c. *Mecistogaster linearis* (F.), ♂, hind-wing. d. The same, fore-wing. e. *Mecistogaster marchali hauxwelli* Selys, ♂, fore-wing. f. Apex of hind-wing of *Microstigma calcipennis* sp. n., ♀. g. The same of *Anomisma terminatum* (McL.), ♀ heteromorph, hind-wing. h. The same of male and andromorph female, hind-wing.

bluish. Thorax black on dorsum to as far lateral as the first lateral suture, blue thereafter except for a moderately broad black stripe on the postero-lateral suture. Narrow antehumeral stripes of azure blue on dorsum; unmarked beneath thorax. Legs entirely black. Wings evenly enfolded a rich olivaceous brown; pterostigma dark yellow with blackish centre and thick black framing nervures, very oblique, about half as long again as broad in fore-wings but nearly twice as long as broad in the hind-wings, covering one and a half to two cells; 15-16 postnodals in fore-wings, 13-14 in the hind-wings; 4 postdiscal cells in all wings; petiolation beginning slightly proximal to the level of the proximal antenodal; Ac about midway between the antenodals; Riv + v arising slightly proximal to subnodus, IRiii at that level; Riii between the 7th and 8th postnodals in fore-wings, and at about the 6th in the hind-wings; IRii at the 10th postnodal. Abdomen black, marked with azure blue as follows:—segment 1 all blue save for a small basal black spot; segment 2 with an irregular ventro-lateral stripe on each side and a large, slightly variable, dorsal spot extending nearly the whole length of segment but falling slightly short of the base; usually this spot is shaped like an egg in an egg-cup, the egg facing basad, but in others it may be subcoarctate, vase-shaped or even approaching that of a clover-leaf. Segment 3 with a moderately broad middorsal stripe tapering from base nearly to apex; segment 4 with or without a short basal blue ring, segments 5 to 8 and 10 entirely black but occasionally the latter with a small subdorsal subapical blue point on each side; segment 9 broadly blue on dorsum from base to apical border. Anal appendages black, superiors longer than inferiors, as long as segment 10, widely divaricate as seen from the dorsum, subcylindrical and ending in a claw-like apical spine as seen in profile. The inferiors broad and short, stoutly conical with the apex directed obliquely upwards and then curled outwards from beneath the superiors: the basal part produced backwards as a short stout spine.

Female. Abdomen 24 mm. Hind-wing 18 mm.

Except for sexual characters and the blue markings of the abdomen, this sex is exactly similar to the male. Segment 2 is usually without the dorsal blue spot but an occasional vestige is present; segment 8 has about the apical third or fourth blue; 9 the apical half but middorsally the blue may extend basad for some distance; segment 10 with the whole of dorsum blue. Anal appendages shortly conical, these and the robust vulvar scales black but the latter, occasionally, bordered above with blue.

Habitat: PERU: Mishuyacu, 11 males and 7 females taken during the months of January, March, June, July and October, so that it evidently occurs all the year round. Females are difficult to distinguish from those of nearly related species but the absence of any marking on segment 2 and the arrangement of the markings on segments 8 and 9 are usually distinctive. As regards the males, the shape and the relative lengths of the anal appendages and the marking on segment 2 are the only sure guides. In Calvert's key in the *Biologia Centrali Americana* this species works out next to *rogersi*.

Argia mollusca sp. n. (fig. 1, j, k and l).

Male. Abdomen 16-18 mm. Hind-wing 24-28 mm.

Head coal black, labium with base cinereous, labrum dark azure blue broadly bordered and traversed medially with black, bases of mandibles blue, genae glossy black. The quadrate blue spot against the eyes opposes the bases of antennae (seen in *A. mishuyaca*) occasionally present but usually much reduced or altogether absent: large blue postocular spots and, finally, a narrow blue bordering of the eyes below. Prothorax black on dorsum, bluish low down on the sides or this area pruinose. Thorax black on dorsum to as far lateral as the first suture, blue thereafter, but this traversed by a broad black fascia on the mes- and met-epimeron, which is itself intersected by the pale postero-lateral suture.

Beneath pale. Legs entirely black. Wings evenly enfumed throughout with olivaceous brown as in *mishuyaca*: pterostigma short, of similar shape in all wings, very oblique, covering only one cell or, in some wings, slightly more than this, black framed finely in golden yellow and dark thick nervures; 4 postdiscal cells in fore-wings, 3 in the hind-wings; 15-17 postnodals in fore-wings, 13-14 in the hind-wings; Riv + v proximal in origin to the subnodus, IRiii at that level, Riii arising at about the 7th postnodal in fore-wings, IRii at the 10th; petiolation begins from the level of the proximal antenodal or a little distal to this in the hind-wings; Ac about midway between the antenodals. Abdomen black, segment 1 broadly azure blue laterally; segment 2 with a blue ventro-lateral stripe on each side and, usually, an oval or diamond-shaped middorsal blue spot which does not extend to either the basal or apical borders of segment; the remainder of abdomen black save for segments 8-10, which are broadly azure blue on dorsum, this colour tapering from apex to base of segment 8 or more rarely confined to the apical third of this segment. There is also a narrow blue ventro-lateral stripe to segments 8-10 which gradually becomes obscured in full aduldage. Anal appendages black, shorter than segment 10, very inconspicuous and crowded together; superiors seen from above have three sides, that of the lower being flat, those of the inner and outer broadly rounded, the appendages being triangularly oval and shallowly emarginate at apex; seen in profile, they are rounded and tapered to an acute apex, from the inner and lower part of which springs the usual stout claw-like apical spine. Inferiors very short and stout, shaped somewhat like a snail-shell but with the apex curled somewhat outwards and overlapping the apical spine of superiors; below and behind a rudimentary spine projects downwards and backwards, representing the conventional apical spine of the genus.

Female. Abdomen 28 mm. Hind-wing 18 mm.

Closely similar to the male but the wings usually less deeply enfumed; the juxta-ocular blue spot often absent; no visible dorsal marking on segment 2; segment 8 entirely blue on dorsum; 9 blue with two large basal triangular black spots which are separated by the blue ground-colour and extend for about half the length of the segment; segment 10 black. Anal appendages shortly conical, black; vulvar scales dark brown. Pterostigma short and of the same size and shape in all wings as in the male.

Habitat: 3 males and 3 females from PERU: Mishuyacu and Florida, during the months of March, May and July, but mostly in March. This species, in its general facies and macroscopically, is remarkably like *mishuyaca* but the shape of the anal appendages and the pterostigma of the same size and shape in fore- and hind-wings will serve to distinguish them. The females may be differentiated by the latter character and by the different distribution of the blue markings on the terminal abdominal segments. The anal appendages of the male do not agree with any other species so far figured; they are very minute and for a correct understanding must be removed from the 10th segment and examined individually as has been done for the present description.

***Argia makoka* sp. n. (fig. 1, a).**

Male. Abdomen 21.5 mm. Hind-wing 19 mm.

Head: labium pale brown, labrum, anteclypeus and a broad transverse band on the frons extending to the level of the bases of antennae and whole of genae pale blue; large postocular spots and a narrow bordering to eyes below are also blue. Prothorax blue with a very broad black middorsal stripe extending from anterior to posterior lobe, the latter being broadly rounded. Thorax black on dorsum to as far lateral as the first lateral suture, marked with a very broad antehumeral stripe on each side which equals the middorsal black in its breadth; laterally blue, without any trace of a black stripe on the second

or postero-lateral suture, this area and beneath being rather heavily pruinosed. Legs entirely black. Wings hyaline, but palely enfumed; pterostigma rather short, about one-third as long again as broad, but slightly longer in the hind-wings, covering only one cell (abnormally one and a half cells in one wing), black framed finely in golden yellow; 16-17 postnodals in fore-wing, 14 in the hind-wing; 4 postdiscal cells in fore-wings, 3 in the hind-wings; petiolation beginning about opposite the proximal antenodal, Ac situated midway between the antenodals, Riii arising between the levels of the 7th and 8th postnodals in fore-wing, at the level of the 6th in the hind, IRii rather far distal, at the 11th or 10th postnodal in all wings. Abdomen black marked with blue as follows:—segment 1 broadly at the sides; segment 2 with a broad black stripe on each side bordered below by blue and enclosing on the dorsum a broad blue spot shaped like a shield with its base resting on the base of segment and its apex extending to the junction of its middle and apical thirds, at which point it is narrowly confluent with an apical triangular spot of blue (this spot is an extension of the spot seen in *A. mishuyaca*); segment 3 with a moderately broad middorsal stripe of blue tapering and extending to just short of apex of segment; segment 4 with a similar stripe but arrested at the basal third of segment; segments 5 to 7 and the whole of 10 black, unmarked; segments 8 and 9 broadly blue on dorsum. Anal appendages black, about as long as segment 10, but the superiors considerably shorter than the inferiors. Seen from above, the superiors are subquadrate with the apical border bevelled inwardly and unnotched; laterally they are unguulate, obtusely pointed at apex, from below and on inner side of which arises a short claw-like spine. The inferiors sloping obliquely upwards and backwards, the lower border sinuous, the superior and inferior apical spines equal in length but the former the more robust and thicker.

Habitat: PERU: Mishuyacu, xi.30, a single male. This species resembles *A. kokama* Calvert in the shape of its appendages although these differ in some measure: the species also differs in its markings as follows:—the absence of the lateral black stripe on thorax, the black on vertex not extending forwards of the level of the antennae, the antehumeral stripes as wide as the middorsal black, segment 4 predominantly black. The abdomen is shorter and the hind-wing longer than in *kokama*. *A. kokama* comes from Iquitos, Peru.

Argia extranea extranea Hagen.

Dr. C. H. Kennedy *in litt.* has informed me that Mrs. Gloyd, who has been engaged now for several years in trying to unravel the species of *Argia*, has expressed the opinion that *A. extranea*, in the Ecuadorian and Peruvian areas, runs into many forms. I had come to somewhat the same conclusions, but suspect that these forms may be a conglomeration of varieties, wet and dry area forms, races and subspecies. Unfortunately we do not know which of these forms was the actual one described by Hagen, and whereas his type lacked practically all blue markings, descriptions of the species by all subsequent authors have given the ground-colour as blue and the sparse markings as black. Among the Peruvian material before me are two different insects, both extremely black and largely devoid of blue markings but with anal appendages generally similar in shape to those described in the type. Thus either of these resembles *extranea* Hagen more closely than do the specimens described by Selys, Williamson, Calvert etc. They may be described as follows:—

Argia extranea forficula subsp. n. (fig. 1, d and e).

Male. Abdomen 27-27.5 mm. Hind-wing 20-21 mm.

Head entirely black save for the moderately large rounded postocular spots. Prothorax black, the lower parts of sides and beneath pruinosed white; thorax black with narrow

blue antehumeral stripes; laterally the usual blue area obscured by a broad black fascia which leaves only the anterior border of mesepimeron and posterior border of metepimeron blue; the lower part of sides and beneath pruinose white. Legs entirely black. Wings hyaline, not enfumed; pterostigma *short*, not longer than broad in all wings, covering only one cell, black. Petiolation beginning proximal to the proximal antenodal; Ac situated about midway between the two antenodals; 16-18 postnodals in fore-wings, 14-15 in the hind-wings; 3-4 postdiscal cells in fore-wings, 3 in the hind-wings; Riii arising opposite the 8th postnodal in fore-wings and at the 7th in the hind; IRiii opposite the 10th postnodal in all wings. Abdomen black save segments 8 and 9, which are broadly blue on the dorsum. Anal appendages black: superiors short, truncate at apex, not notched; inferiors twice the length of superiors and with superior and inferior apical spines of equal length, the former robust, triangular in profile, directed straight upwards, not curled at apex, the latter directed straight back and running parallel with its fellow, thus resembling somewhat the appendages of an earwig. Segment 10 raised at apical border and deeply notched at each side.

Habitat: PERU: Balsapuerto, Rio Paranapura, 220 m. Two males ii.33. The above description tallies well with Hagen's *Agrion extraneum*, but the anal appendages are closely similar to those of *extranea* of other authors. The short pterostigma with costal side equal to the distal is also common to the latter and appears to me to be an important character, separating it at once from the following subspecies. The extremely restricted blue markings distinguish it from *A. extranea* Selys et auct.

***Argia extranea euphorbia* subsp. n. (fig. 2, e, f and g).**

Male. Abdomen 28 mm. Hind-wing 18.5 mm.

Head: labium black; labrum blue with the anterior border and a small median spot projecting from the base black; bases of mandibles blue, rest of head black save for the large rounded postocular spots. Prothorax black, bluish on the lower parts of sides; posterior lobe broadly rounded. Thorax black on dorsum to as far lateral as the first lateral suture, marked with narrow blue antehumeral stripes; laterally blue, changing to white below and beneath and marked along the length of the postero-lateral suture with a narrow black stripe. Legs entirely black. Wings evenly enfumed throughout with olivaceous brown; pterostigma elongate, rather more than half as long again as broad in all wings, covering from one and a half to two cells, black; 15 postnodals in fore-wings, 13 in the hind-wings; 4 postdiscal cells in all wings; Ac situated slightly nearer the distal antenodal; petiolation beginning proximal to the proximal antenodal; Riii arising at the level of the 6th postnodal; IRiii at the 9th. Abdomen black, segment 1 blue laterally; segment 2 with a longitudinal lateral stripe on each side and an oval blue spot on dorsum extending from base to slightly beyond the middle of segment; segments 3-7 unmarked; 8 to 10 broadly blue on dorsum, the latter segment deeply notched and tuberculate at apical dorsal border. Anal appendages black, equal in length to segment 10; superiors broadly and shortly conical as seen from the dorsum, notched at apex, the outer border of notch prolonged into a short obtuse spine; inferiors broad at base, the lower border in profile very sinuous, the superior and inferior apical spines of equal length and robustness, the former strongly recurved at apex, the latter directed straight back in line of abdomen.

Habitat: PERU: Mishuyacu. A single male, 10.viii.30. This description again tallies with that of Hagen's *Agrion extraneum*, especially in regard to the anal appendages, so that it may well be Hagen's species. The elongated pterostigma separates it from the preceding subspecies, which it otherwise closely resembles in general appearance. Calvert thinks that the blue markings

of Hagen's type have faded; none is mentioned in the description nor are there any extensive blue markings in this subspecies.

Aeloagrion flammeum (Selys).

There are 13 males and 16 females of this common species in the collection, all very typical. It is widely distributed throughout the Amazonian basin; all the present specimens were collected in PERU: Mishuyacu, from April to August.

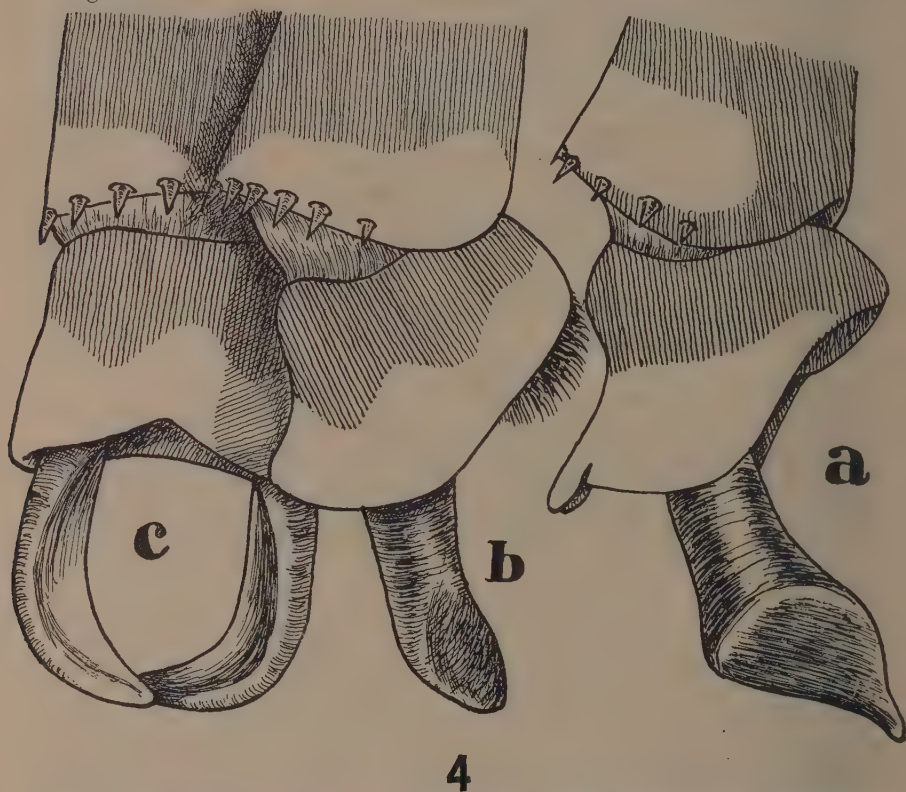


FIG. 4.—Male anal appendages of: a. *Mecistogaster marchali hauxwelli* Selys, right lateral view. b. *Mecistogaster linearis* (F.), right lateral view. c. The same, dorsal view.

Family PROTONEURIDAE.

Protoneura protostictoides sp. n.

Male. Abdomen 34 mm. Hind-wing 18.5 mm.

Head: labium pale brown, labrum glossy dark green metallic with anterior border finely margined with yellow, epistome and frons pale, but a narrow green metallic band traversing the anteclypeus. Rest of head dark steely metallic; beneath head and eyes dull black. Prothorax dark metallic green on dorsum, pale laterally. Thorax dark metallic green on dorsum to as far as the postero-lateral suture and the upper part of

metepimeron. Rest of sides and beneath thorax palest blue. Legs pale, darkening at distal ends of femora and on extensor surfaces. Wings hyaline, 11 postnodals in fore-wings, 9 in the hind-wings; CuP ending slightly distal to the level of vein descending from nodus; 2 postdiscoidal cells; Riv + v arising proximal to subnodal vein, IRiii from that vein; Riii arises at the level of the 4th postnodal and IRii at the 8th in fore-wings; pterostigma slightly longer than deep, its sides parallel, covering only 1 cell, yellow with dark greyish centre. Sectors fused at origins, arculus slightly distal to the 2nd antenodal. Abdomen very long and very slim, segments 7 and 8 dilating steadily towards end of abdomen, segments 1 and 2 dark metallic green on dorsum, rest of abdomen dark reddish-brown (but probably black or even steely metallic in the full adult). (Segments 9 and 10 missing in the type.)

Habitat: PERU: Mishuyacu. A single male, 16.vi.30, the type will be deposited in the British Museum (Natural History). This species closely resembles a *Protosticta* Selys in its facies and fragile build. It differs from *P. capilliformis* Selys by its larger size and higher nodal index. It differs from other species of the Selysian Group 1 by the whole of the dorsum of thorax dark metallic (although there is some indication of a short, upper posthumeral pale stripe) and the quadrate pterostigma, the costal side being but a fraction shorter than the posterior. *P. ephippigera*, which resembles it in this latter respect, has the whole of the sides and beneath thorax black; the nodal index and size are also less. This species might be the male of *P. humeralis*, but the shape of the pterostigma is altogether different.

***Protoneura peruviansis* sp. n. (fig. 5, a and b).**

Male. Abdomen 29 mm. Hind-wing 19 mm.

Head: labium straw yellow, labrum yellow with a median basal point and the outer edges finely black; anteclypeus yellow, postclypeus steely black, frons and genae pale, rest of head dark bronzed black. Prothorax and thorax dark bronzed green to as far out as the first lateral suture; rest of sides and beneath pale yellow or pale blue. Posterior lobe of prothorax very prominent, rounded. Legs yellow, distal ends of femora, two narrow rings on same, distal ends of tibiae and whole of tarsi black. Wings hyaline, 11 postnodals to fore-wings, 10 in the hind-wings; pterostigma slightly longer than wide, covering 1 cell, yellow with dark clouded centre which leaves a golden yellow frame between it and the thick bordering black nervures. CuP ending at the vein descending from the nodus, Riv + v arising proximal to subnodus, IRii distal to that vein, the two veins approximating immediately thereafter. Abdomen brownish-black with dull coppery reflex and poorly defined pale basal interrupted rings on segments 3-7. Anal appendages: superiors about half the length of segment 10, broadly conical as seen from above, the apex abruptly narrowed; seen in profile, they are shaped somewhat like a horse's head, the apex of the segment projecting straight backward, resembling the ears, whilst a long robust ventral spine forms the muzzle, the extreme apex of this being slightly recurved forwards. Inferior appendages slightly longer, very robust and broadly conical as seen from any aspect.

Habitat: A single male from PERU: Mishuyacu, 2.vii.30. The type will be deposited in the British Museum (Natural History). The shape of the anal appendages will distinguish this species from any others in the genus. The origins of Riv + v and IRii place it in the 2nd Group, which fact separates it from the previously described species belonging to Group 1. It resembles *P. sancta* in some respects, but differs by the absence of a pale juxta-humeral stripe and also by the projecting posterior lobe of prothorax (depressed in

sancta). The male of this latter species has not so far been described, so that comparisons can be made only with the female.

Protoneura tenuissima Selys (Bates MSS.).

In this specimen the middorsal thoracic stripe is a beautiful dark purplish metallic, as also is the posterior lobe of prothorax (black in the type). The abdomen is slightly shorter, but beyond these two points, I can find no other differences. The nodal index is similar, viz., 12 postnodals to fore-wings, 10 in the hind-wings.

1 female, PERU : Mishuyacu, 29.i.31.

Family PSEUDOSTIGMATIDAE Tillyard & Fraser.

Division *Pseudostigmatina* Kirby, 1890, *Cat. Odon.* : 119.

Subfamily PSEUDOSTIGMATINAE Munz, 1919, *Mem. Amer. ent. Soc.* 3 : 20.

Family PSEUDOSTIGMATIDAE Tillyard & Fraser, 1938, *Aust. Zool.* 9 : 158.

Six species in three genera belonging to this aberrant group are represented in the Leeds Museum collection; I include here also the description of one new species, the holotype of which has been in my own collection for some years and which was determined as new by Dr. E. Schmidt during a visit to this country in 1938.

Apart from the exaggerated specialisation of the pterostigmal area of the wings and the enormously elongated abdomen, the PSEUDOSTIGMATIDAE are characterised by their unusually long petiolation of the wings, the elongate subrectangular shape of the discoidal cell, which is almost typical of the MEGAPODAGRIIDAE, and finally by the frequent appearances of supernumerary antenodals, as well as, in at least one species, cross-veins to the discoidal cell and cubital space. All of these characters point to an evolution parallel to that of the MEGAPODAGRIIDAE and towards the AMPHIPTERYGIDAE.

The larvae, so far as they are known, breed in the leaf-bracts of Bromeliads, and the elongated abdomen is an adaptation for this purpose, enabling the imago to insert its ovipositor into the deep and narrow clefts and to reach far down to the small cisterns of water which have formed below. In a country like Amazonia, it seems at first sight to be an anomaly that insects should choose such restricted watery habitats in which to breed, but further consideration suggests that the vast annual flooding of the low-lying country so dilutes down the food-supplies that the insects may find it impossible to obtain even a bare existence. In the tiny rain-water cisterns formed by the Bromeliads, vast numbers of mosquito and other dipterous larvae breed and it is on these that the Pseudostigmatine nymphs thrive.

Genus *Mecistogaster* Rambur, 1842.

Mecistogaster marchali race *hauxwelli* Selys (fig. 3, a and e, fig. 4, a).

This species was discovered about 1880 by Hauxwell, the veteran South American ornithologist and described by Selys in 1886, since which year it does not appear ever to have come to light again, probably because little collecting has been done in Peru. I find 3 males and 2 females among the Leeds material which do not differ at all widely from the type. The pterostigma of the fore-wing in the male is broadly oval in shape (not squared as in *M. marchali*), a bright primrose yellow but palely reddish ochreous at its circumference, and

covers 3 rows of cells, with 12 to 16 cells in the first row, 10 to 12 in the second and about 9 in the third which abuts on the first intercalated vein of the wing. A fine reticulation of cells encloses the pterostigma to as far as the vein Rs and is of the same bright primrose yellow as the pterostigma.

Distribution: The present material comes from PERU (Mishuyacu), and was taken in the second half of January 1931.

Mecistogaster ornatus Rambur, 1842.

This beautiful species, which is generally regarded as rare, is represented by one very teneral male and four adult females, the former from Yumbatos, -ix.31, the latter from Balsapuerto, -v.32, San Antonio, -i.32 and Mishuyacu, 7.vi.31, 13.iii.31, respectively. The adult females have the wings tinted evenly

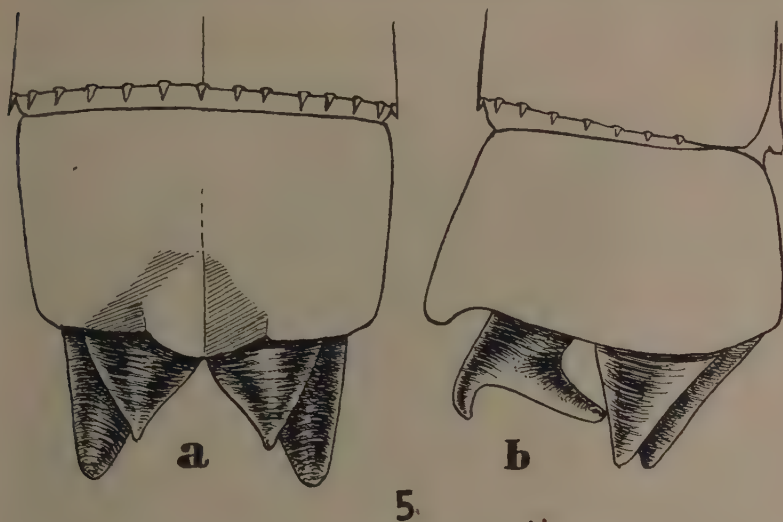


FIG. 5.—Male anal appendages of *Protoneura peruviansis* sp. n., a. Dorsal view. b. Right lateral view.

throughout with palest brown, but on the outer fourth of the wing, proximal to the apical opaque spot, the brown forms an areola around each cell, the whole effect of which is to darken distinctly this area in strong contrast to the rest of the wing. The opaque spot is squared inwardly, rounded posteriorly where it abuts on to Rs and is finely edged with black; the spot itself, which is a rich tangerine orange in colour above and below on the fore-wing, but only above in the hind, overlaps a second opaque semilunar spot at the extreme apex of the wing, which extends as far as the level of Riv + v and is a dusky carneous by direct, and chalky white by transmitted, light. Beneath the hind-wing, the apical coloured spot is a dull carneous. The females are of large size and approximately of the same dimensions as those given by Selys: abdomen 85 mm. and hind-wing 65 mm.

Distribution: Mexico, Guatemala, Honduras, Nicaragua, Panama, Colombia, Venezuela, Guiana, Brazil, Costa Rica and Peru.

Mecistogaster jocaste vicentius Ris.

The type of this species was described in 1916 and came from Colombia; there have been no further records of it since. Eight specimens are present in the Leeds collection, unfortunately all females. Generally they are much larger than the Ris specimens and they differ in at least one important character, viz., the absence of the pterostigma in the fore-wings of fifty per cent of the specimens. In four specimens no vestige can be made out; in another there is only a partial darkening of one or two cells; whilst in the rest there is darkening and more or less organised chitination of from 2 to 5 cells on the costal border near the apex of the fore-wings. The dimensions vary from 46 to 50 mm. for the hind-wing, and 61 to 67 mm. for the abdomen, these being considerably higher than those given for *jocaste* or its subspecies *vicentius*. It is possible that we are dealing with but a single species the make-up of which is as yet in a very fluid condition.

Distribution: COLOMBIA: Umbria, 24.xii.30 to 10.i.31; Villavicencio, vi.1910, i.1911.

Mecistogaster linearis (F.) (fig. 3, c and d, fig. 4, b and c).

About 60 examples of this species are present in the Leeds material, one-third only of which are males. They represent all age states from very teneral examples with pure white unorganised pterostigma to full adults with fully chitinated, black pterostigma. Some of the intermediate males are difficult to distinguish from the same sex of *modestus* Selys, whilst those of the female sex may be similarly confounded with the same sex of *hauxwelli* Selys. In some of the males there is a distinct bulging of the pterostigma, although not nearly to the same extent as is seen in *marcbali* or *hauxwelli*; this has to be discounted in making the determinations. Ris's table for distinguishing *linearis* from *modestus* functions fairly well in practice but this applies only to the female sex. A male from Mishuyacu has an additional cross-vein in the cubital space and probably indicates a previous branching of the anal trachea, as is common to the higher Zygoptera. Several of the females have the wings evenly and rather deeply enfumed; this may be an indication of age, but I do not think so, because the pterostigma, even in the hind-wings, does not show any trace of black. I name such forms provisionally as var. *infumata* var. n. The great variations in the pterostigma and the size of insects commented upon by previous authors is again exhibited in the present material.

Distribution: COLOMBIA, Umbria: ♂, 28.xi.30; Florida, 2 ♀, 13.iii.31, ♂♀, 17.iv.31; PERU: Iquitos, ♀, 3.vi.31, ♂♀, 18.vi.31; Balsapuerto, ♀ teneral, 1.iii.31; Putumayo R., ♂, 3.iv.31; Mishuyacu, 12 ♂, from 7.ii.31 to 10.vii.31, 27 ♀ from 25.i.31 to 20.xii.31, Yumbatos, 1 ♂, x.31. Specimens appear to have been taken in all months save September and October.

Microstigma rotundatum Selys.

This species is probably the most commonly met with of all the family PSEUDOSTIGMATIDAE; thus there are over one hundred examples in the present material, the males being in slight preponderance. I have not been able to demarcate from typical *rotundatum* the two races *exustum* Selys and *lunatum* Selys, but find examples of each which have been taken in the same locality. Four examples which I possess from the Morton collection, labelled "Ampiacara R." without further data, may be determined as 2 *rotundatum*, 1 *exustum* and 1

as *lunatum*. The great majority of the present material fall into typical *rotundatum* and such as have the apical brown fascia restricted are mostly teneral, so that I am of opinion that examples of the two races are more often than not mere evidence of varying age states. As is usual, great differences in the dimensions of individuals are met with, and I find as much as 1.5 inches in difference in the expanse and at least 1.0 inch in the length of the abdomen. The colour of the opaque apical spot varies from bright primrose yellow to a dull carneous tint. An important character which has not been noted before is the presence of accessory antenodal cross-veins or "secondaries." These are present only in the costal space, thus differing from the "primaries" in being incomplete; they are present in at least 8 per cent of the specimens and in the fore-wings only, mostly situated between the two primaries or more rarely proximal to the primaries. The presence of these supernumerary veins strongly suggests a relationship to the MEGAPODAGRIDAE and AMPHIPTERYGIDAE.

***Microstigma calcipennis* sp. n. (fig. 3, f).**

Female. Abdomen 70 mm. Hind-wing 53 mm.

Head : labium, genae and anterior border of labrum narrowly yellow, rest of head dull black. Behind head pale yellow, this colour sharply defined from the black of occiput. Prothorax black dorsally and subdorsally, a pair of pure white spots on each side. Thorax dull black on dorsum and as far lateral as midway between the lateral sutures; a fine posthumeral stripe of yellow and an equally narrow black stripe bordering the postero-lateral suture, which broadens in its superior third. Remaining parts of sides and beneath creamy yellow but obscured below by pruinescence. Coxae and trochanters pale yellow, the rest of legs missing. Wings hyaline save the apices, which are a pure chalky white especially when viewed by transmitted light, over a space beginning on the costa of fore-wings about 9 cells proximal to the pterostigma, and in the hind-wing about 8 cells, extending obliquely and convexly inwards with slightly serrate border to the level of IRiii or Riv+ v, where these veins reach the apical border of wings. The pterostigma is small, made up of 3 cells in fore-wings but of only a single cell in the hind-wings; it is of dark opaque blackish-brown and thus strongly contrasted with the pure white apex of wing. In the fore-wing the pterostigma is trapezoidal in shape and about half as long again as deep, with the opposite sides parallel, whilst in the hind-wing it is subtriangular, the distal and proximal sides converging posteriorly, the former side being strongly oblique. The wing membrane adjacent to the opaque white apex is tinted with brown; this colour gradually fading out towards the middle of wing. Reticulation, including the costa, reddish-brown above, black beneath wings; no supernumerary antenodals present, 2 rows of cells in the costo-radial space at apices of wings, 60 postnodal veins, reticulation in opaque area of apices not closer than elsewhere and white as for that area. Abdomen dark reddish-brown on dorsum, deepening to dull black on segments 2 and 6 to 10, pale yellow beneath. Ovipositor and the shortly conical anal appendages black.

Distribution : BOLIVIA. The holotype, which is a female, is in my collection and was received in 1934 together with other species belonging to the same family, and without further data. It will eventually be presented to the British Museum (Natural History).

***Anomisma terminatum* McLachlan (fig. 3, g and h).**

The present collection contains much valuable material belonging to the genus *Anomisma* McLachlan, which is one of the most interesting and strangest in the Order Odonata. Its characters are unique in several respects; thus

terminatum McLachlan, the genotype, is the only species of the superfamily Coenagriioidea in which the discoidal cells are split up or traversed by cross-veins, the pterostigma is absent in all wings of both sexes, the discoidal cell is enormously prolonged distally and extends beyond the level of the nodus, the cubital space is traversed by several cross-veins, one of which appears to be analogous to the basal cubital cross-vein of the PLATYSTICTIDÆ, secondary antenodal veins are quite common, and lastly the petiolation of the wings extends to the level of the nodus. The arrangement of the extra cross-veins in the cubital space appears to have taken on a certain conformity although there are frequent exceptions. Normally the true tracheal crossing, Ac, is

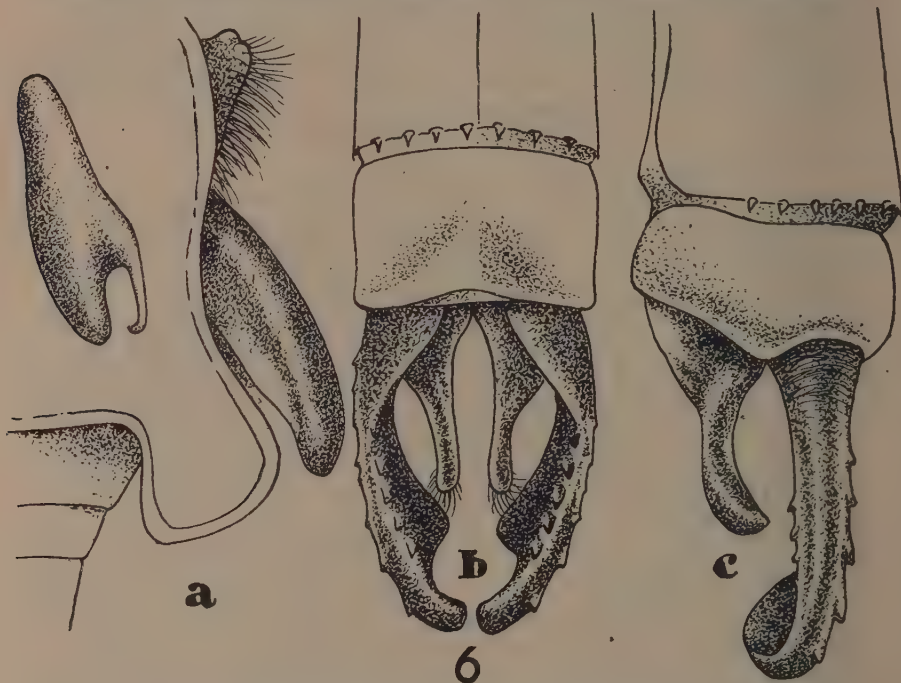


FIG. 6.—a. Male genitalia of *Uracis reducta* sp. n. b. Male anal appendages of *Megapodagrion megalopus* Selys, dorsal view. c. The same viewed from the left side.

situated slightly distal to the level of the basal primary antenodal or, less rarely, midway between the primaries; a basal supernumerary cubital cross-vein lies just proximal to the basal primary, whilst 3 other supernumeraries are situated distally below the outer half of the discoidal cell and are prolongations of 3 cross-veins traversing that structure. Some specimens show these 3 replaced by 2 wider spaced cross-veins. The secondary antenodal veins show no particular consistency in their location. In one male, right and left fore-wings have such a vein between the nodus and outer primary, the right hind-wing has 1 vein in a similar position and the left 2; a female has a secondary present between the primaries in the left fore-wing only; a second male has a vein between the primaries in the right and left fore-wings and 1 proximal to the

basal primary in the right fore-wing; a third male has one between the primaries in the right fore-wing and one between the distal primary and nodus in the left fore-wing; another female has a vein between the nodus and primary in the right fore-wing, a similar in the right hind-wing as well as one between the primaries, one between the nodus and primary in the left fore-wing and one between the primaries in the hind-wing of the same side. Of the 23 specimens in the Leeds collection, 8 males and 2 females have secondary antenodals present, but all confined to the costal space. In general, it may be said that the arrangement of these veins most closely assimilates to *Neurolestes* and that if the genus was dissociated from the rest of the PSEUDOSTIGMATIDAE, then most systematists would have little hesitation in placing it among the MEGAPODAGRINIDAE. Another rare character of the species is disclosed by this new material, and that is the existence of two different forms of the female, one being an andromorph and distinguished from the male only by sexual characters, the other a heteromorph, which was the one described as the allotype female. Of the 12 females before me, 7 are andromorphs and 5 heteromorphs, all the latter conforming to type and differing only in cases where the specimens are teneral and the black bands correspondingly paler and narrower.

Distribution: PERU: Iquitos, ♂, 13.vi.31, ♀, 13.i.31, Mishuyacu, ♂, 3.vi.30, ♂, 9.iv.30, ♂, 31.i.31, ♂, 8.iv.31, ♂, 2.iii.31, ♂, 11.vi.30, ♂, 28.xi.30, ♂, 28.v.30, ♀, 24.i.31, ♀, 13.xii.30, ♀, 2.vi.30. COLOMBIA: Umbria, ♂, 27.xii.39, ♂, 6.i.31, ♂, 10.i.31, ♀, 31.xii.30, ♀, 18.xi.30. The type is from Ecuador, and is now in the British Museum.

Family MEGAPODAGRINIDAE.

Two genera and three species are represented in the Leeds Museum collection, viz. *Megapodagrion* Selys with two species and *Heteragrion* Selys. Unfortunately, with one exception, all are females and as this sex is very homogeneous throughout the family, some difficulty has been met with in the determinations.

Megapodagrion megalopus (Selys) (fig. 6, b).

A single male and two females, all from PERU: Mishuyacu, 17.vii.30, 13.viii.30 and 28.xii.30. The male is fully adult, the females nearly so, therefore it is possible to add a few details to the original descriptions which appear to have been made from teneral examples.

The postnodal index varies from 18 to 21 in the fore-wings, and 16 to 18 in the hind-wings; the pterostigma of the male, which was described as yellow, is actually blackish-brown, covering rather more than 2 cells; in the female it is creamy yellow framed heavily in black nervures, and this pale colour undoubtedly persists in this sex, whilst it is present in the male only during the teneral stage. The postdiscal cells vary from 2 to 3 in the fore-wings, but are constant at 2 in the hind-wings. The ground-colour of the adult male at least is dove-grey or slatey-blue; the middorsum is uniform dark brown, bordered by a paler humeral fascia, which bears two or three large squarish dark brown spots, evidently a vestigial interrupted stripe. At the upper end of the humeral suture, there is a small sharply defined black spot; a second smaller black spot is found on the first lateral suture at the junction of its upper and middle thirds, and this suture is finely black above the spot. The second lateral suture bears a broad black oblique stripe; a sinuous ill-defined line runs across the mesepimeron from above just behind the humeral black spot, to below where it joins a black Y-shaped marking; finally the metepimeron has its central portion suffused with dark brown. Segments 9 and 10 of the abdomen are chalky white in the male, reminding one of a similar marking in the oriental *Caliphaea confusa* Selys; these same segments

in the female are dull ochreous but segment 9 has a large quadrate spot at the base on each side and a triangular basal marking on the dorsum dark chocolate brown.

Megapodagrion setigerum Selys.

A single female from PERU: San Antonio, i.33, agrees closely with the original description and calls for no special remarks.

Heteragrion sp. Group *aurantiacum* Selys.

One female from S.E. COLOMBIA: Florida, 13.iii.31, and 2 females from N. PERU: Yumbatos, Huallaga Region, xi.32, G. Klug coll.

These females, which work out to Group *aurantiacum* Selys, agree so closely with some species of the Group type which I possess that I do not think there

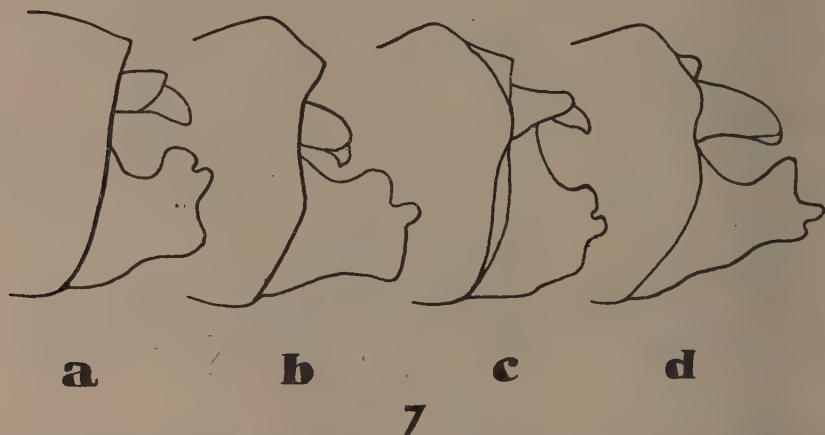


FIG. 7.—Outline of the apex of segment 10 and the anal appendages of: a. *Argia pulla* Hagen. b. *Argia frequentula* Calvert. c. *Argia gaumeri* Calvert. d. *Argia infrequentula* sp. n. (a, b, and c after Calvert.)

can be much doubt about their determination; they certainly differ much more strongly from several other species with which I have been able to compare them, all of which were determined by the late Bruce Williamson. Unfortunately nearly all my specimens are males, and as females of the genus are very homogeneous it is not possible to be entirely certain as to their determination. The two females from Yumbatos show some differentiation in their pterostigmas, the costal side in one being longer than the proximal side, and, in the other, shorter than the proximal side; apart from this character, they are entirely similar.

Suborder Anisoptera.

This suborder is represented in the present collection by species belonging to the Families AESHNIDAE, GOMPHIDAE and LIBELLULIDAE. The GOMPHIDAE are represented by only one species and the CORDULIDAE and CORDULEGASTERIDAE by none at all as was to be expected from families which form but a fraction of the Central American fauna. The AESHNIDAE in the collection

have already been dealt with by Mr. Hincks (1934, *Ent. Rec.* **46** : 77) and it will suffice here merely to list the species with their country of origin :—

Coryphaeschna adnexa (Hagen), PERU.
Triacanthagyna ditzleri Williamson,
 PERU.

Triacanthagyna satyrus Martin, PERU.
Gynacantha tenuis Martin, PERU.
Gynacantha auricularis Martin, PERU.
Gynacantha klegesii Williamson, PERU.
Gynacantha nervosa (Rambur), PERU.
Gynacantha litoralis Williamson, PERU.

Gynacantha gracilis (Burmeister),
 PERU.

Gynacantha membranalis Karsch, PERU
 and COLOMBIA.

Neuraeschna producta Kimmins, PERU.

Staurophlebia reticulata Burmeister,
 PERU and COLOMBIA.

Staurophlebia gigantula Martin, PERU.

Family GOMPHIDAE.

Agriogomphus sylvicola Selys.

PERU, COLOMBIA and BRAZIL.

Family LIBELLULIDAE.

Ten genera with 26 species have been determined amongst the rich material at my disposal; whilst some of the species are rare, only a single one has been found new to science, a rather aberrant species of *Uraxis* Rambur.

Libellula herculea Karsch.

4 ♂, 4 ♀, PERU : Mishuyacu, 17.i.31, 25.vi.30, 12.vii.30, 30.vii.30 and 6.xii.30; Iquitos, 2.v.31 and 6.vi.31. A not uncommon species with a wide distribution; it is one of the enormous equatorial forms which are among the largest and most robust dragonflies known.

Orthemis ferruginea (Fabricius).

About 60 specimens of this ubiquitous species, all of which, save one, are from PERU : Mishuyacu and Yumbatos, and were taken in every month throughout the year. The males, as usual, far outnumber the females, the latter being taken only when they come to water to oviposit. One female from COLOMBIA : Umbria, 28.xi.30. The species is a dominant one and occupies the same place in the neotropical fauna as does *Orthetrum sabina* (Drury) in the tropics of the Old World.

Orthemis biolleyi Calvert.

4 ♂, 2 ♀, PERU : Mishuyacu, 25.vi.30, 23.viii.30 and 17.xii.30; Balsapuerto, 1.v.31. COLOMBIA : Umbria, 18.vi.31 and 9.xi.30. The type comes from Costa Rica but the distribution is probably over the greater part of Central and northern South America, including the Amazonian basin. Not a common species, judging from the paucity of Museum specimens.

Orthemis cultriformis Calvert.

12 ♂, 11 ♀, PERU : Mishuyacu and Yumbatos; COLOMBIA : Umbria. The specimens were collected throughout the year, the seasonal incidence being continuous. A moderately common species with a distribution from Panama to Brazil.

Dasythemis esmeralda Ris.

6 ♂, 4 ♀, PERU: Mishuyacu and COLOMBIA: Umbria, specimens being taken in the months of January, February, June, August, November and December, so that it would appear to occur throughout the whole year. The species is a rare one and known only from very few specimens; the distribution is Peru and Ecuador, the type from the former country. The present specimens agree closely with Ris's descriptions.

Zenithoptera americana (L.).

8 ♂ and 1 ♀, from PERU: Mishuyacu and Balsapuerto; COLOMBIA: Umbria. According to the data on these specimens, the species has a long season extending from October to May inclusive. Not uncommon; distributed throughout northern S. America.

Perithemis thais Kirby.

2 ♂, from PERU: Balsapuerto, iii.33 and v.33. Not differing from type; found apparently throughout the Amazonian basin as far inland as its headwaters.

Genus *Uracis* Rambur.

The present collection emphasises the dominant character and extraordinary rich development of the genus *Uracis* Rambur, of which five out of the six described species as well as one new species are represented. Of these, *siemensi* Kirby, *ovipositrix* Calvert, *infumata* Rambur, *fastigiata* (Burmeister), *imbuta* (Burmeister) and the new species all occur in Peru, whilst *siemensi*, *fastigiata* and *imbuta* are found also in Colombia.

Uracis siemensi Kirby.

9 ♂, 9 ♀, PERU: Mishuyacu, and COLOMBIA: Umbria, all collected during July, August and December. Apparently a local species in parts of the Amazonian basin. Bates stated that: "It was common in both wet and dry seasons and common in pathways of the forests in dry months." Both forms, with hyaline and coloured wings, are represented.

Uracis ovipositrix Calvert.

16 ♂, 12 ♀, all from PERU: Mishuyacu, with a seasonal occurrence similar to the last. Common throughout the Amazonian basin and extending well into Brazil. The specimens call for no particular remarks.

Uracis reducta sp. n. (fig. 6, a).

Male. Abdomen 24 mm. (with appendages). Hind-wing 29 mm.

Head: labium pale yellow, labrum olivaceous brown paling to a lighter yellow along anterior border; anteclypeus and the two frontal facets greyish, rest of head, including occiput, dark blackish-brown. Prothorax dark brown on dorsum, ochreous laterally. Thorax with dorsum and shoulders as far lateral as the first lateral suture dark blackish-brown, finely striated with ochreous after the usual *Uracis* pattern; rest of sides and beneath olivaceous green. Legs ochreous, spines, the knees of hind legs, flexor surfaces of all tibiae and the tarsi black. Wings hyaline with the apices deeply infuscated as far proximal as inner end of pterostigma, the latter dark yellow framed in heavy black nervures and

covering about $2\frac{1}{2}$ cells; only a single supplementary cubital cross-vein in all wings, nodal index— $\frac{8-11\frac{1}{2}}{9-10} | \frac{12\frac{1}{2}-10}{10-8}$, hypertrigones and discoidal cell of hind-wing entire, that of fore-wing traversed once; subtrigone of fore-wing 3-celled; discoidal field of fore-wing with 2 rows of cells to beyond level of nodus; a single row of cells between anal-loop and hind border of wing, broadening to 2, then 3 rows at base of wing; the anal-loop open as in species of *Zyxomma* Rambur and *Tholymis* Hagen, ending squarely on posterior border of wing. Abdomen dark ochreous, changing rather abruptly to black at level of jugal suture on segment 3. Anal appendages: superiors nearly twice the length of segment 2, sloping strongly downwards, slim and cylindrical at base, broadening towards apex and then tapering again to a finely pointed apex. A distinct subapical heel present ventrally which bears 3 small, closely-set spines on its free border. Inferior appendage brownish ochreous, triangular, as long as the superiors. Genitalia: lobe depressed, obtuse, lamina truncate, sharply angulated to transverse axis of segment, hamules projecting, as long as the lamina which they tend to overlap apically, inner hamules elongate slim hooks lying parallel with and slightly separated from the outer hamules by a deep notch (fig. 6, a).

Habitat: PERU: Mishuyacu, a single male 31.v.31. *Type* will be deposited in the British Museum (Natural History). This new species lies nearest *ovipositrix*, from which it is easily separated by the much narrower base of the hind-wing with only a single row of cells between the anal-loop and the hind border (3 rows in *ovipositrix*).

Uracis infumata Rambur.

4 ♂, 8 ♀, all from PERU: Mishuyacu, collected during the months of January, February, July and August, and perhaps double-brooded. An uncommon species with distribution confined to the Amazonian basin and Bahia. All are quite typical.

Uracis fastigiata (Burmeister).

7 ♂, 1 ♀, PERU: Mishuyacu and Yumbatos; COLOMBIA: Umbria. A common species found throughout the year and with a wide distribution throughout the whole of northern South America and Trinidad. A smaller form, perhaps a distinct species, is found in Central America. The present specimens conform to the larger southern form.

Uracis imbuta (Burmeister).

13 ♂, 4 ♀, PERU: Mishuyacu, during July and August; COLOMBIA: Umbria, during January, to March and June and July; Honduras, from February to May. A widely distributed and common species, found throughout the northern parts of South America and Central America.

Micrathyria didyma laevigata Calvert.

3 ♀, PERU: Mishuyacu, 29.i.31, 13.vii.30, and 15.viii.30. Two only of the three specimens have the discoidal cell free, the third has this in the fore-wing traversed once. Possibly they belong to the more common race *didyma didyma*, the venation being notoriously unstable. Whilst *didyma* is more or less confined to Central America and Cuba, *laevigata* inhabits the Amazonian basin, Colombia and Brazil.

Micrathyria dido Ris.

A single pair from PERU : Florida, 24.iii.31. The type male is from Para : two females in the Selysian collection are labelled "Guiana or Brazil"; the latter locality is probably the correct one, although both may be incorrect. The present specimens agree closely with Ris's description and figure of genitalia.

Erythrodiplax castanea (Burmeister).

12 ♂, 7 ♀, PERU : Mishuyacu, and COLOMBIA : Umbria, occurring in every month of the year. A common and widely distributed species reported from the Amazonian basin, Ecuador and Brazil. One of the present specimens bears data—PERU : Balsapuerto, Rio Paranapura, 220 m.

Erythrodiplax connata fusca (Rambur).

5 ♂ and 1 ♀, PERU : Mishuyacu, 4.ii.31, 4–12.iii.31; British Guiana, 15.i.12. A species even more common and with a wider distribution than the last. Extends into Trinidad and southwards to as far as Buenos Aires. I can find no report of its capture in Peru, although it occurs in Ecuador, Colombia and Venezuela.

Erythrodiplax kimminsi Borrer.

A single male from PERU : Mishuyacu, 8.viii.30. Reported from Costa Rica, Venezuela, Colombia, Panama, Ecuador and the Amazonian basin but not hitherto from Peru. The specimen agrees well with Borrer's figures of the genitalia etc.

Erythrodiplax basalis basalis (Kirby).

1 ♂ and 2 ♀, PERU : Mishuyacu, 10.vi.31, 14–15.viii.30. A locally common species found in many parts of the Amazonian basin and northern South America. Not so far reported from Peru. The present specimens are quite typical.

Erythrodiplax attenuata (Kirby).

A single male from PERU : Yumbatos, -.ix.32. A moderately common species confined mainly to the Amazonian water system but extending southwards into Brazil.

Erythrodiplax amazonica melanica Borrer.

1 ♂ from PERU : Mishuyacu, 14.iii.31. So far only reported from the Amazonian basin; not so far reported from Peru.

Erythrodiplax unimaculata (De Geer).

3 ♂, 8 ♀, PERU : Mishuyacu, collected during the last eight months of the year but probably occurring in every month. A widely distributed, dominant species, found throughout Central and northern South America and the West Indies. The present examples do not differ from type.

Erythrodiplax ochracea ochracea (Burmeister).

3 ♂, 6 ♀, PERU : Mishuyacu, and COLOMBIA : Umbria, collected during the first eight months of the year. The specimens agree more closely with the

typical race rather than with *aequatorialis* Ris, from the lower waters of the Amazon. A common and widely distributed species.

Erythrodiplax connata ines Ris.

A single male from PERU : San Antonio, -iv.33, is determined as this race of *connata* with some considerable doubt. The type is from Ecuador but the species was originally described from Bolivia as *E. connata* by Calvert; it has also been reported from Peru.

Erythemis haematogastra (Burmeister).

A single female from PERU, Mishuyacu, 20.iv.31. A common and widely distributed species but not hitherto reported from Peru. Extends into Central America, West Indies and southwards to Brazil.

Lepthemis vesiculosa (Fabricius).

8 ♂, 1 ♀, PERU : Mishuyacu, from November to March. One of the most dominant American dragonflies, extending from Central America and the West Indies southwards to the Argentine. Bates's note on this species may be quoted : "A very abundant species met with throughout the country (Amazonia) in open and semicultivated places, its flight is excessively rapid but it settles frequently." In its dominant nature, coloration and unusual build it resembles to a remarkable degree the common *Orthetrum sabina* Drury of the Old World tropics.

Macrothemis pumila Karsch.

One pair from PERU : Iquitos, 8.vi.31, 2 ♀, Mishuyacu, 4.vi.30, 14.viii.30; 2 ♀ from COLOMBIA : Umbria, 8.vii.31, 10.xi.30. This small and beautiful species is not common in collections, probably on account of its habits of flight, concerning which Bates stated : "It flew in open spaces in the virgin forest Aveyros, flying high but slowly and hovering to and fro for hours without settling." This is an uncommon habit in the LIBELLULIDAE but reminiscent of the Corduline *Idionyx* Hagen of the Old World. In size and colouring, it is an exact copy of the tropical *Tetrathemis platyptera* Selys, but the habits of the two are very different. I possess 1 ♂ and 5 ♀ collected by Jesse Williams at Manaos and Porto Velho, 22.ii. and 16.vi.22, State of Amazonas, Brazil.

Misagria parana Kirby.

A single male from PERU, Mishuyacu, 7.ii.31, which agrees closely with type. The species is rare in collections and probably very local. Bates stated that it was found in "Pathways in the forest, Santarem." "Depth of forest, 29.xi.48." The present record is a new one for Peru.

NOTE.

Since the above was written, I have received the following note from Mr. W. D. Hincks :— "In addition to the material reported in the present paper and in the previous contribution (1946, *Trans. R. ent. Soc. Lond.* 96 : 11) the collection also contained about 8 species of GOMPHIDAE of the genera *Epi-gomphus*, *Gomphoides*, etc. (besides the single male *Agriogomphus sylvicola* Selys,

discussed by Col. Fraser in 1943) and, I think, 3 species of CORDULIIDAE (*Neocordulia batesi* Selys, *Aeschnosoma forcipula* Hagen, and a probably new species of the latter genus). This material was set and therefore did not survive the bombing of the Leeds Museum in 1941 as did most of the papered specimens which have been studied by Col. Fraser. I believe one or two specimens of the supposed new *Aeschnosoma* are still in the hands of another specialist to whom they were submitted before the war. W. D. HINCKS."

BIBLIOGRAPHY.

- RAMBUR, P., 1842, *Ins. Nèvrop.*
 SELYS-LONGCHAMPS, E. de, 1853, *Syn. Calopterygines* (sep.).
 —, 1854, *Mon. Calopterygines* (sep.).
 —, 1859, *Add. au Syn. Calopterygines* (sep.).
 —, 1860, *Syn. Agrionines, 1me Legion* (sep.).
 —, 1862, *Syn. Agrionines, 2me Legion* (sep.).
 —, 1865, *Syn. Agrionines, 3me Legion* (sep.).
 —, 1869, *Second Add. au Syn. Calopterygines* (sep.).
 —, 1873, *Trois Add. au Syn. Calopterygines* (sep.).
 HAGEN, H. A., 1875, *Proc. Boston Soc. nat. Hist.* **18** : 20.
 SELYS-LONGCHAMPS, E. de, 1876, *Syn. Agrionines, 5me Legion* (suite) (sep.).
 —, 1877, *Syn. Agrionines, 5me Legion* (suite et fin) (sep.).
 —, 1886, *Rev. Syn. Agrionines*, Brussels.
 KIRBY, W. F., 1889, *Trans. zool. Soc. Lond.* **12** : 249, pls. 51-7.
 —, 1890, *Cat. Odonata.*
 —, 1897, *Ann. Mag. nat. Hist.* (6) **19** : 598-617.
 CALVERT, P. P., 1898, *Proc. Boston, Soc. nat. Hist.* **28** : 301, pl. 1 & 2.
 —, 1899, *An. Mus. nac. B. Aires* **7** : 25.
 KIRBY, W. F., 1899, *Ann. Mag. nat. Hist.* (7) **3** : 362.
 CALVERT, P. P., 1901, *Biol. cent.-Amer.* **11**, *Neurop.* (1901-1908).
 —, 1902, *Bull. Mus. comp. Zool.* **39** : 103, pls. 1 & 2.
 RIS, F., 1904, *Odonaten, Hamb. Magalb. Sreise* **14** : 1-44.
 —, 1908, *Dtsch. ent. Z.* **1908** : 518.
 CALVERT, P. P., 1909, *Ann. Carneg. Mus.* **6** : 73.
 RIS, F., 1909, *Cat. Coll. Selys, Libellulinen* **9-16** : 1-(1909-1913).
 —, 1913, *Mem. Soc. ent. Belg.* **22** : 55-102.
 FÖRSTER, F., 1914, *Arch. Naturgesch.* **80** (A) **2** : 59.
 NAVÁS, L., 1915, *Mem. R. Acad. Barcelona* (11) **27** : 1-26.
 —, 1915, *Ent. Mitt.* **4** : 146.
 KENNEDY, C. H., 1916, *Ent. News* **27** : 325, pl. 18.
 WILLIAMSON, E. B., 1917, *Trans. Amer. ent. Soc.* **43** : 211.
 RIS, F., 1918, *Arch. Naturgesch.* **82** (A) **9** : 197, pls. 1 & 2.
 SJÖSTEDT, Y., 1918, *Ark. Zool.* **11** (15) : 1-14.
 RIS, F., 1928, *Konowia* **7** (1) : 40.
 LONGFIELD, C., 1929, *Trans. ent. Soc. Lond.* **77** : 125.
 RIS, F., 1930, *Misc. Publ. Mus. zool. Univ. Michigan* **21** : 1-50, pl. 1-4.
 HINCKS, W. D., 1934, *Ent. Rec.* **46** : 77.
 BORROR, D. J., 1942, *Ohio St. Univ. Biol. Ser.* **4** : 1-286, pls. 41.
 FRASER, F. C., 1943, *Proc. R. ent. Soc. Lond.* (B) **12** : 161.

Vol. 97. Part 19. Pp. 473-496, 27 figs.

3rd December, 1946.

IMP. INST. ENT.

LIBRARY

3 DEC 1946

Eu. 344

THE

TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

X HINTON, H. E., B.Sc., Ph.D., F.R.E.S. The "gin-traps" of some beetle pupae; a protective device which appears to be unknown 473-496, 27 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1946-1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.

C. B. WILLIAMS, M.A., D.Sc. } *Vice-Presidents*.

H. B. WILLIAMS, LL.D.

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.

J. W. EVANS, M.A., D.Sc.

G. FOX-WILSON, N.D.H.

R. M. GREENSLADE.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

CAPT. R. A. JACKSON, R.N.

MISS C. E. LONGFIELD.

SIR GUY A. K. MARSHALL, K.C.M.G.,

D.Sc., F.R.S.

G. E. J. NIXON, B.A.

J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.

FRANCIS HEMMING, C.M.G., C.B.E.

H. E. HINTON, B.Sc., Ph.D.

W. RAIT-SMITH.

O. W. RICHARDS, M.A., D.Sc.

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., Ph.D.

B. M. HOBBY, M.A., D.Phil.

J. F. PERKINS, B.Sc.

J. SMART, B.Sc., Ph.D.

W. H. THORPE, M.A., Sc.D.

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.

K. G. BLAIR, D.Sc.

O. W. RICHARDS, M.A., D.Sc.

N. D. RILEY (*Secretary*).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.

E. A. COCKAYNE, M.A., M.D., F.R.C.P.

CAPT. R. A. JACKSON, R.N.

COL. F. A. LABOUCHERE.

A. M. MASSEE, D.Sc.

THE HON. MIRIAM ROTHSCHILD.

W. H. THORPE, M.A., Sc.D.

N. D. RILEY (*Secretary*).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO :

1. **British National Committee for Biology** (Royal Society).

Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.

Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.

2. **Local Committee of Management of Wicken Fen.**

Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].

3. **National Trust for Places of Historic Interest or Natural Beauty.**

Mr. H. M. Edelsten, O.B.E., appointed 1944.

4. **New Forest Association.**

Mr. W. Fassnidge, appointed 1934.

5. **New Forest Joint Committee.**

Mr. W. Fassnidge, appointed 1939.

Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.

6. **Royal Meteorological Society. Phenological Committee.**

Dr. C. B. Williams, M.A., D.Sc., appointed 1937.

7. **Council for the Promotion of Field Studies.**

Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.

8. **Joint Bioclimatic Committee.**

Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.

Dr. C. B. Williams, M.A., D.Sc., appointed 1945.

THE "GIN-TRAPS" OF SOME BEETLE PUPAE; A PROTECTIVE DEVICE WHICH APPEARS TO BE UNKNOWN

By H. E. HINTON, B.Sc., Ph.D., F.R.E.S.

Department of Entomology, British Museum (Natural History).

Manuscript received 17th May, 1946.

(Read 2nd October, 1946.)

WITH 27 TEXT-FIGURES.

CONTENTS.

	PAGE
Introduction	473
II. Median gin-traps	
A. Single median gin-traps	477
1. DERMESTIDAE	477
2. PTILODACTYLIDAE	485
3. DRYOPIDAE	486
B. Paired median gin-traps	488
1. SCARABAEIDAE	488
2. CERAMBYCIDAE	488
III. Lateral gin-traps	490
IV. Discussion	491
Postscript	494
Acknowledgments	495
References	496

INTRODUCTION.

WITH very few exceptions the pupae of the Holometabola are concealed in cells or cocoons of one kind or another which serve to protect them from their enemies and in some measure also protect them from adverse physical changes in their environment. The cuticle of most of the pupae thus concealed is thin and flimsy, affording little or no protection against any enemies which may succeed in breaking into the cell or cocoon. The Lepidoptera and orthorrhaphous Diptera are notable exceptions in that their pupal cuticle is fairly heavily sclerotised and obtect, and is, moreover, in the primitive terrestrial forms of both orders armed with sharp spines and tubercles of various kinds. Although at first sight it might appear that the hard and spiny cuticle of these groups was acquired for protection, this is most certainly not the case, as I have shown elsewhere (Hinton, 1946b). Their hardened, obtected, and spinose cuticle was acquired in the first instance to enable the adults to propel themselves, when ready to emerge, to the surface of the ground or any other material in which the cells or cocoons were enclosed; and such protective value as accrued to these pupae by reason of their hardened and spinose cuticle was only of incidental or secondary importance. When the pupal cuticle is hardened and obtected, it nearly always remains in this condition (the cyclorhaphous Diptera are a notable exception) even though the imagines evolve

new methods of escape from the cell or cocoon in which the pupal cuticle plays no part. Thus it is probably true to say that, as regards the pupal cuticle of the higher Lepidoptera, factors which were in the first instance of only incidental selective value later became of prime importance in preserving and even increasing the hardness of the pupal cuticle.

Since there are relatively few pupae which have dispensed altogether with cells or cocoons, which are the primitive method of protection, considerable interest attaches to each instance. It is obvious that so long as pupae are concealed in cells or cocoons they are not subject to change through selection for cryptic or mimetic purposes; and the dull uniform colour of pupae so concealed is in striking contrast to the rich variety of colour of exposed pupae of butterflies and beetles.

Broadly speaking, pupae that are exposed tend to have the cuticle more heavily sclerotised than related forms which are concealed. It appears certain that the exposed pupae of the Lepidoptera and orthorrhaphous Diptera acquired the character of being obtect and strongly sclerotised, not for protection, but while they still possessed cells or cocoons, in order to enable the imagines to emerge. The pupae of the Coleoptera which are obtect and heavily sclerotised acquired these characters while in the process of losing their cells or cocoons or after these were lost. With the exception of the STAPHYLININAE only, all beetle pupae which are enclosed in cells or cocoons are feebly sclerotised and exarate.¹ With the exception of many Chalcidoidea, this generalisation is also true of the Hymenoptera. If a few beetles which pupate in damp and very sheltered places, *e.g.* the LATHRIDIIDAE, are excepted, it appears that all those which are exposed on leaves, stems, or other objects are heavily sclerotised and often obtect, *e.g.* most COCCINELLIDAE and many CHRYSOMELIDAE.

When the cuticle of a pupa is strongly sclerotised for protection or primarily to enable the imago to escape, it is nearly always also obtect; and obtect pupae are always well sclerotised as compared with related non-obtect forms. The only exception to this rule that I know of are the pupae of some COCCINELLIDAE and CHRYSOMELIDAE, which are heavily sclerotised but not obtect. All pupae which are strongly sclerotised or obtect may be placed in one of three groups according to the origin of these characters:—

1. To enable the imago to escape from its cell or cocoon (Lepidoptera, orthorrhaphous Diptera).
2. For protection when the cell or cocoon is discarded (PTILIDAE, CORYLOPHIDAE, COCCINELLIDAE, many CHRYSOMELIDAE).
3. For additional protection while still enclosed in a cell or cocoon (STAPHYLININAE. The Chalcidoidea possibly also belong here).

Exposed pupae are protected in a number of ways in addition to having a hardened cuticle with the appendages usually gummed down. Very many pupae are more or less protected from enemies by their form or colour or a combination of both. The latter may so resemble their background that they remain unnoticed by possible predators or, like some COCCINELLIDAE which have an unpleasant taste, they may be sufficiently conspicuous to escape being mistaken for an edible species before they have been bitten and thus seriously

¹ Some HISPINAE (CHRYSOMELIDAE), which pupate within their larval mines, are heavily sclerotised and sometimes also obtect, but there is good reason to believe that these characteristics were acquired by the exposed pupae of their ancestors and that the habit of pupating in their larval mines or otherwise concealed is a secondary or derived habit (Hinton, 1946b).

injured or killed. A few pupae are protected because they closely resemble an insect or other animal which, for one reason or another, is itself immune from attack.

A few Lepidopterous pupae which are enclosed in cocoons stridulate (to scare off enemies?). For instance, the pupa of an Oriental Hesperid, *Gangara thyrasis* Fabricius, makes a loud hissing noise by moving so that its roughened proboscis rubs the walls of ridged grooves on the ninth and tenth abdominal segments. This species also makes a loud rattling noise by rubbing its body against the surface of its pupal cell, as does a British Agrotid, *Pseudoips bicolorana* Fuessly, by rubbing its abdominal setae against the walls of its parchment-like cocoon. But the ability to produce sound does not appear to have been recorded for any exposed pupae.

Nearly all exposed pupae are capable of wriggling more or less violently when stimulated. The abdomen may, for instance, move rapidly up and down, from side to side, or it may describe an ellipse. Different groups of beetles and butterflies often have their own characteristic movements, but the precise relation of these movements to the physical or biological factors of their environment is largely unknown. Some of the exposed pupae of the CASSIDINAE, which have numerous long spines, may wriggle in such a way as to thrust their spines into an attacker, but this possibility does not appear to have been investigated.

All previously recorded protective devices of pupae are of a more or less passive kind, and it is therefore of considerable interest to note that the pupae of the common mealworms, flour beetles, and skin beetles, as well as some that are less known, have the adjacent margins of one or more pairs of abdominal segments modified to form a simple but effective device for pinching insects that may attack them. These pinching organs or gin-traps are of two chief kinds: (1) the median gin-traps of the DERMESTIDAE, PTILODACTYLIDAE, DRYOPIDAE, SCARABAEIDAE, and CERAMBYCIDAE; and (2) the lateral gin-traps of the TENEBRIONIDAE. The difference in position of the two kinds of gin-traps appears to be related to a difference in the way the pupae move when stimulated.

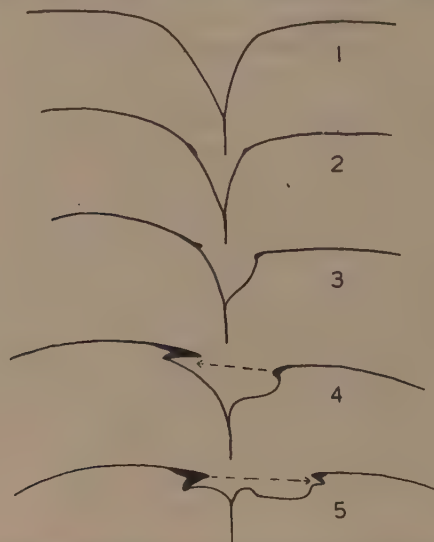
II. MEDIAN GIN-TRAPS.

Although structural variations of specific, generic, or even family importance are exhibited by the median dorsal gin-traps of the DERMESTIDAE, PTILODACTYLIDAE, DRYOPIDAE, SCARABAEIDAE, and CERAMBYCIDAE, all are constructed on the same general plan. Each gin-trap consists of two strongly sclerotised toothed or smooth plates or ridges which may be likened to the jaws of a gin-trap. The anterior jaw is near the posterior margin on one segment, and the slightly or very differently shaped posterior jaw is near the anterior margin of the segment immediately behind. When the pupa is relaxed, the abdomen is curved downwards and the jaws of each gin-trap are held widely open. When the pupa is stimulated, the abdomen is bent upwards and the segments are partly telescoped into each other so that the jaws meet or overlap.

The circumference of each abdominal segment is less where it is joined to the segment behind or to that in front than it is at the middle (figs. 1-5); and this is true of all segments except some of the most posterior. The result of this is that the region near the posterior margin of one segment and that near the anterior margin of the segment immediately behind is always depressed. Where the gin-traps are present, the depression between the segments and

under the jaws is nearly always deepened and broadened and its margins are sometimes very well defined (figs. 22-23).

The function of a depression or pit between the jaws is clear enough. Without a pit between them the jaws would less often be able to secure a firm grip on the palpi, legs, or other appendages of an attacking arthropod. The presence of a pit makes it possible to insert an appendage so that it may be firmly gripped by the pupa. In some instances the pit might even enable the jaws of the trap to close on an intersegmental membrane. A simple experiment will suffice to demonstrate the utility of the pit. If two razor-blades are placed on a flat surface and a match held upright between them, it will be found that when the edges of the blades are brought together they will nearly always slide under the end of the match without gripping it. This is because the end of



FIGS. 1-5.—(1-3) Hypothetical evolution of a gin-trap. (4) *Dermestes maculatus* Degeer. (5) *Dryops luridus* Erichson.

the match is not absolutely flat, as neither are the ends of the appendages of an animal likely to attack the pupa. If the experiment is repeated so that the razor-blades meet over a pit wide enough to accommodate the match, the blades cannot fail to grip the match, and their edges can only meet by cutting through the match.

The dorsal median gin-traps may be single, as are those of the DERMESTIDAE, PTILODACTYLIDAE, and DRYOPIDAE, or they may be paired, as are those of the SCARABAEIDAE and CERAMBYCIDAE. The PTILODACTYLIDAE and DRYOPIDAE are closely related families, and it is possible that both are derived from a common ancestor possessing gin-traps. In all others, however, it is clear that the gin-traps are independently developed, so that there is no doubt that median and lateral gin-traps have been evolved no less than five different times. Furthermore, so few pupae have been available for this study, that it is more than likely that gin-traps will be discovered in other families of beetles.

The gin-traps are in all cases confined to the abdomen, for the simple reason

that only the abdominal segments can be moved by the pupa. The muscles which enable the pupa to wriggle its abdomen are carried over directly from the larva and are complete at the time the pupal cuticle is being laid down, when their tonofibrillar attachments are secured. It appears that these muscles are not subject to extensive histolytic or phagocytic action, but maintain their integrity into the adult stage. After the imaginal cuticle is laid down and the insect is, properly speaking, an adult, it remains invested by the now effete pupal cuticle for a considerable time. During the whole of this period, which is often as long as or longer than the pupal period, the gin-traps on the pupal cuticle are used by the adult in precisely the same way as they were previously used by the pupa.

A. *Single median Gin-traps.*

1. DERMESTIDAE.

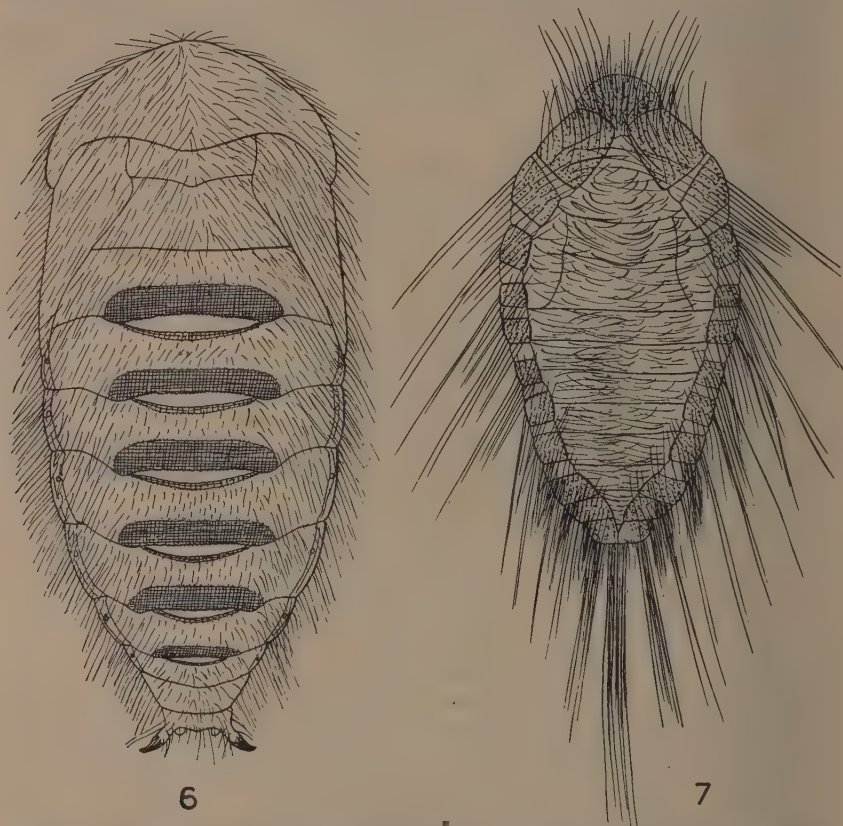
The number of Dermestid pupae and pupal skins available is sufficient to show clearly that as new habits and structures which serve to protect the pupa are acquired the number of dorsal gin-traps is reduced. The existence of a relationship of this kind cannot be demonstrated without a brief exposition of the phylogeny of the family.

The species of DERMESTIDAE are placed in six subfamilies, viz. : DERMESTINAE, ORPHILINAE, TRINODINAE, ATTAGENINAE, THYLODRIINAE, and ANTHRENINAE. Of these I have been unable to examine pupae of the primitive ORPHILINAE or those of the THYLODRIINAE, which as regards many adult characters are highly specialised. Of the remaining four subfamilies, the ANTHRENINAE are unquestionably the most specialised, as is evident from the morphology and feeding habits of both the larvae and adults (Hinton 1945 : 242-3); and, if the number of recent species is any indication, they are by far the most successful group of the family.

Although the adults of the DERMESTINAE lack a median ocellus, in all other important particulars of the morphology and habits of both larvae and adults the DERMESTINAE appear to retain a greater number of primitive features than any other subfamily. It is difficult indeed to believe that the median ocellus was secondarily acquired in the family and that it is possible to derive groups possessing a median ocellus from an ancestor lacking such an organ. It must therefore be admitted that the archetype of the DERMESTIDAE possessed a median ocellus and that the DERMESTINAE are the only group which has lost the ocellus in spite of the fact that it has in most respects diverged less from the ancestral Dermestid than has any other group. If all characters are taken into account, the TRINODINAE and ATTAGENINAE are intermediate between the primitive DERMESTINAE and the highly specialised ANTHRENINAE. The ATTAGENINAE are second only to the ANTHRENINAE as regards numbers of recent species, and, as in the latter subfamily, many of their larvae are capable of digesting keratins and their adults feed apparently only on pollen and nectar. These facts suggest that they may be more specialised than the TRINODINAE, which are a smaller and relatively unsuccessful group. However, as regards habits of pupation and structure of pupae the ATTAGENINAE are rather close to the DERMESTINAE and the TRINODINAE close to the ANTHRENINAE.

When ready to pupate, the mature larva of *Dermestes* will bore into almost any compact material that happens to be near. The larval burrow may be only long enough to conceal the pupa or may be a foot or more in length. The pupa often sheds the last larval skin completely, and this skin and the debris made by the larva when boring usually block the entrance to the pupal

chamber. When indoors, the larvae frequently pupate in more or less exposed situations on or near their food material, and the larval skin is often not completely shed but remains and partly encloses the pupa. The larval skin splits along the median longitudinal line of the thorax and also along the coronal suture and each of the frontal sutures, so that the resulting fracture is Y-shaped with a long stem. The partly shed skin entirely covers the posterior third of the dorsum and all of the ventral and lateral parts of the



FIGS. 6-7.—(6) Dorsal view of *Attagenus gloriosae* F. (7) Same of *Anthrenus vorax* Waterhouse enclosed in the last larval skin.

abdomen, but the whole of the head and all or nearly all of the thorax are exposed. If the pupa is stimulated and caused to wriggle a few times, the larval skin is completely shed; and in cultures and normal infestations many pupae are found which have entirely shed the larval skin.

The pupation habits of the ANTHRENINAE are very different indeed. The mature larva pupates where it has been feeding—in dried insects, among hair or feathers, etc.—and never burrows into wood or any other compact material in order to make a pupal chamber. The larval skin fractures as in *Dermestes*,

but the median longitudinal split is continued backwards to the posterior margin of the sixth and sometimes even to the posterior margin of the eighth abdominal tergite. The pupa never sheds the larval skin. Its ventral surface, sides, and dorso-lateral parts are always covered so that only the dorsum of the head, thorax, and abdomen is exposed (see fig. 7).

The discussion below on the reduction of the number of gin-traps is based on the assumption that the method of pupation of *Dermestes* is the most primitive in the family and that of the ANTHRENINAE the most highly specialised. But this assumption is not made solely because the majority of the characters of all stages show that the DERMESTINAE are more primitive than the ANTHRENINAE, for it is not uncommon to find that groups which are on the whole very primitive may nevertheless possess some very highly specialised features. With few exceptions, the pupae of the Holometabola are enclosed in cells or cocoons made by the larvae, and in all instances where a different method of protection is used this is clearly newly acquired or secondary. The pupae of all the families related to the DERMESTIDAE (whether they are regarded as belonging to the Dascilloidea *s. lat.* or the Cleroidea) are protected by cells of one kind or another and are not found in exposed places nor do they remain within the larval skin.

The difference in the method of pupation that exists between the primitive and specialised Dermestids is related to a great difference in their habits out-of-doors. The larvae of most of the species of *Dermestes* usually attack carcasses of fish, birds, and mammals lying in fields and woods, whereas the larvae of all or nearly all other Dermestids are normally found out-of-doors only in fairly sheltered places—under bark, in crevices in wood and rocks, in caves, in nests of birds and rodents, and so on. The larval skins containing the pupae are not attached in any way, but in the sheltered places where they are found they are not likely to be blown about by the wind and are protected from the sun and usually also from the rain.

At first sight it might appear that the gin-traps were developed for protection as the habit of pupating in cells was lost, but I do not think that this is the case. The pupae of the Ptilodactylidae, Dryopidae, Scarabaeidae, and Cerambycidae which possess dorsal gin-traps, as well as their relatives without these structures, are always found in cells. In the DERMESTIDAE it is precisely in those pupae that are never found in cells but do remain within the last larval skin that the gin-traps are greatly reduced in number or even lost altogether.

The species of *Dermestes* have five gin-traps, situated on segments 2-3, 3-4, 4-5, 5-6, and 6-7. The ATTAGENINAE (*Attagenus* L.) have six gin-traps, situated on segments 1-2, 2-3, 3-4, 4-5, 5-6, and 6-7. The ATTAGENINAE never appear to make cells in which to pupate.² Their pupae may partly or completely shed the larval skin, as do individual pupae of *Dermestes* when their larvae pupate in sheltered places without making cells. From the evidence available it is not possible to claim that the possession of six gin-traps is a more primitive feature than the possession of five. Except for the fact that the adults have a median ocellus, it may be said that the ATTAGENINAE are more specialised than the DERMESTINAE; their larvae lack urogomphi, often have more specialised hairs, are able to digest keratins, are found out-of-doors usually only in sheltered places, apparently never pupate in cells, and their adults feed on pollen and nectar and not on the same food as their larvae.

² This kind of fact is seldom recorded. Further study may show that some do make pupal cells.

As regards structure, it is not possible to say that the pupae of the ATTAGENINAE are in all respects more specialised, but their hairs are often denser, longer, and more like those of the ANTHRENINAE. Their habits of pupation are certainly more specialised, being intermediate between the DERMESTINAE and ANTHRENINAE, but nearer the former.

In the ANTHRENINAE some genera (*Trogoderma* Berthold, *Anthrenocerus* Arrow) have three dorsal gin-traps which are on segments 1-2, 2-3, and 3-4, whereas other genera (*Megatoma* Herbst, *Thaumaglossa* Redtenbacher, *Anthrenus* Geoffroy) have none. *Anthrenus* larvae have the spear-headed setae arising from secondarily modified areas of the abdominal tergites, many feed more or less exclusively on keratins, and the adults have nearly all the hairs flat and scale-like and their antennae frequently have less than 11 segments—all characters which suggest that *Anthrenus* is the most specialised genus of the subfamily.

The pupal hairs of *Dermestes* are sparser and relatively shorter than those of *Attagenus*. In some species of *Attagenus* the hairs are very long, fine, and very dense. In both *Dermestes* and *Attagenus* the hairs are unevenly distributed, and in both genera they are often denser on the dorso-lateral sides of the body than elsewhere. In both genera they are usually distinctly sparser on the median dorsal area of the abdomen. In neither of the two genera, however, are the hairs of the ventral surface sharply differentiated from those of the dorsal surface. In the ANTHRENINAE, on the other hand, the parts of the body that are covered by the larval skin have the hairs very much shorter than those parts which are normally exposed. In *Anthrenus*, for instance, the areas of the dorsal surface which are exposed are densely clothed with long, fine hairs which are sometimes so entangled that they form a thick protective mat, whereas the sides and ventral surface only have very short, erect, and inconspicuous hairs. The pupae of the TRINODINAE (*Trinodes* Dejean) are in these respects similar to the ANTHRENINAE, and like *Anthrenus*, they have also lost the gin-traps.³ I think no one will quarrel with the view that the gin-traps are independently lost in the TRINODINAE and some ANTHRENINAE as one result of developing similar methods of protecting their pupae.

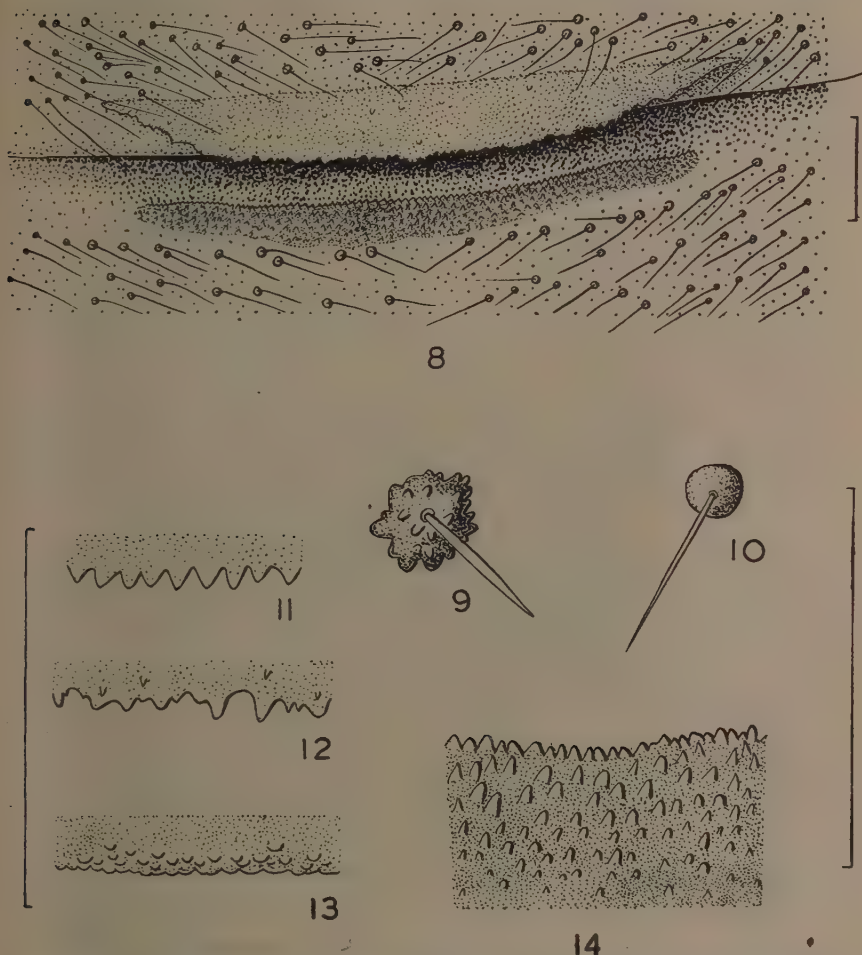
From the facts mentioned in the foregoing discussion it is possible to reconstruct in a broad general way the chief steps in the reduction of the number of gin-traps as new methods of protecting the pupae are acquired.

1. Adults and larvae feed on the same materials, usually carcasses of animals lying in the open. Essential sterol for larva is cholesterol; usual moisture content of food considerably over 20%; larvae incapable of completing their development on foods having a moisture content of 15% or less. A pupal cell is always made in the ground, wood, etc. Adult with a median ocellus, simple hairs, 11-segmented antennae of which the last three segments form a large compact club. Larvae with six ocelli on each side of the head, 4-segmented maxillary palpi, well-developed urogomphi on the ninth abdominal segment, and with only simple hairs. Pupae with five or six dorsal gin-traps; dorsal hairs not arising from tubercles; larval skin always completely shed and split so that longitudinal fracture is confined to the thorax or at most includes the first abdominal segment. (Hypothetical ancestor of all recent DERMESTIDAE.)

2. Species begin to infest materials in sheltered places such as caves or

³ An empty cuticle of the last larval instar of *Hexanodes hudsoni* Blair (TRINODINAE) is available. The longitudinal fracture is confined to the thorax. This fact, together with the way the segments are telescoped, suggests that the pupa is only partly enclosed in the larval skin and may therefore possess gin-traps.

nests of birds and rodents, where they are able to survive if the larvae fail to construct a pupal cell whether for lack of suitable materials or for some other reason. Pupal hairs become more developed on dorso-lateral surfaces,



FIGS. 8-14.—(8) First gin-trap of *Dermestes lardarius* L. (9) One of the tubercles near the middle of the metathorax of *Dermestes peruvianus* Cast. (10) Same of *D. lardarius* L. (11) Middle part of the posterior margin of the anterior jaw of the first gin-trap of *D. peruvianus* Cast. (12) Same of *D. lardarius* L. (13) Same of *D. maculatus* Degeer. (14) Middle section of posterior jaw of first gin-trap of *D. lardarius* L. Lines next to these and other text-figures refer to a length of 0.20 mm.

the ventral surface being protected by the substrate and the dorsal surface by the gin-traps and also by developing a large heavily sclerotised tubercle at the base of each dorsal hair. (Type represented by *Dermestes*, the adults of which, however, have lost the median ocellus.)

3. Species more or less confined to sheltered places. Distinct pupal cell never made. Pupae often do not completely shed the larval skin so that the posterior part of the abdomen remains enclosed; dorsal setiferous tubercles (like those of *Dermestes*) never acquired, or, if acquired, now lost.

4. Species similar to above except that: (1) adults no longer feed on larval food but on pollen and nectar; (2) larvae of some evolve an enzyme capable of digesting keratins; (3) for some larvae sitosterol becomes an alternative for cholesterol; (4) larvae are able to accommodate themselves to food having a very low moisture content, 15% or less; (5) urogomphi lost in larvae but retained in pupae; and (6) pupae tend to develop long silky hairs which cover certain areas with a protective hair-mat. (Type represented by recent ATTAGENINAE.)

5. Pupae more completely enclosed by larval cuticle which therefore splits more extensively,⁴ the median longitudinal fracture extending posteriorly to include several of the abdominal segments.

6. Pupae completely enclosed by the last larval skin, which splits from the frontal sutures to the posterior margin of the sixth to eighth abdominal tergites and leaves only the middle dorsal areas of the body exposed. Urogomphi probably lost at this or the preceding stage. (Ancestral TRINODINAE and ANTHRENINAE.)

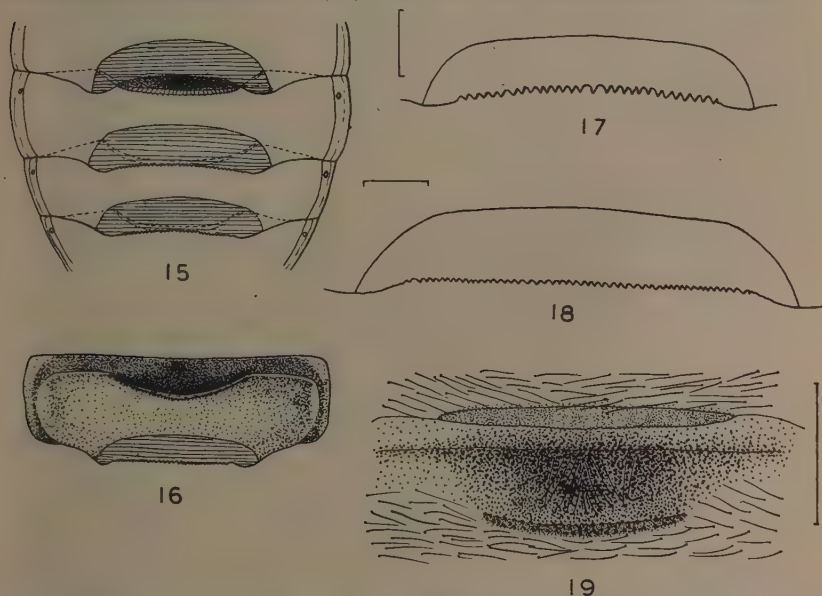
7. Gin-traps gradually reduced in number as the hairs on the exposed dorsal surface become longer and therefore more efficient in protecting the exposed parts. The gin-traps are finally lost in genera (*Trinodes* and *Anthrenus*) of two very different groups the common ancestor of which may be as primitive as that of stage "3" or "4."

At some stage, possibly at "5" or "6," the larvae of the ANTHRENINAE became highly specialised in two further directions: the segments of the maxillary palpi were reduced from four to three and the larvae evolved "segmented" spear-headed setae which are structurally more complex than any other known insect setae. As previously mentioned, some ANTHRENINAE (*Trogoderma* Berthold, *Anthrenocerus* Arrow) still preserve three gin-traps. When these pupae are stimulated they wriggle so that the gin-traps are closed and opened. *Anthrenus*, which has entirely lost the gin-traps, will not wriggle even when pricked hard enough to be seriously damaged (*A. vorax* Waterhouse was the species pricked) or even killed. In some species of *Thaumaglossa*, e.g. *T. bimaculata* Arrow, which are predators on Mantid oothecae, the last larval skin bears very long, fine, white hairs on each side of the dorso-median line. These hairs meet and are entangled above the exposed part of the pupa so that a fairly thick silky mat is formed. The exposed parts of the pupa are thus protected by both pupal and larval hairs. These hairs probably also prevent the pupa from accidentally falling out of the larval skin. From the number of larval skins available it is not possible to determine the instar in which these hairs first appear, but they are relatively much longer in the final instar than in those preceding.

Broadly speaking, the progressive specialisation of the DERMESTIDAE results in a progressive conservation of energy in the period of life between the fully

⁴ The pupae and larvae of the DERMESTIDAE have approximately the same volume. As the pupa assumes the imaginal shape, it is forced out of the larval skin which stretches only to a limited extent. If the pupa remains enclosed, the splitting of the larval skin is much more extensive in order to accommodate the pupa. In many insects the pupa remains enclosed in the last larval skin, which does not split. In such cases, however, the volume of the pupa is appreciably less than that of the larva, e.g. in the STRATIOMYIDAE; and the shape of the larval skin does not appreciably alter.

fed larva and the emergence of the adult. In the primitive Dermestids, e.g. *Dermestes*, an appreciable amount of energy is expended in making a pupal cell. In all species a certain amount of energy is spent when the pupa wriggles and closes and opens its gin-traps. In some, e.g. *Anthrenus*, the gin-traps are lost altogether and the pupa cannot be stimulated to wriggle, so that a further amount of energy is saved. It is likely that any energy saved after the larva stops feeding is advantageous to the species either because it reduces the amount of food required for metamorphosis or because it enables the adult to survive longer or lay eggs without feeding. In this connection it is of interest to note that the species of *Dermestes* will not lay until they have fed on materials rich in proteins, whereas in the highly specialised ANTHRENINAE the females will



FIGS. 15-19.—(15) First three gin-traps of *Attagenus gloriosae* F. First trap slightly open, second and third traps closed. (16) Fourth abdominal tergite of the same species. (17) Anterior jaw of first gin-trap of *Attagenus schäfferi* (Herbst). (18) Same of *A. pellio* L. (19) First gin-trap of *Trogoderma versicolor* (Creutzer) drawn from a cast skin.

lay before feeding and in some, e.g. *Trogoderma versicolor* (Creutzer), the fecundity and longevity of the female is not impaired by lack of food or water (Norris, 1936).

The Dermestid pupae that were examined for this study are included in the key and the list given below. Of the 21 available species, six were represented only by the shed pupal cuticle, and each of these is marked with an asterisk.

Key to Dermestid pupae.

1. Abdomen with two large urogomphi on ninth segment and with five or six well-developed gin-traps. Pupa not or only partly enclosed in the last larval cuticle which is split so that the median longitudinal fracture is nearly always confined to the thorax and very rarely extends to the posterior margin of the first abdominal segment 2.

- Abdomen without urogomphi and with not more than three gin-traps. Pupa always enclosed in the last larval cuticle so that only its middle dorsal surface is exposed; last larval cuticle split so that the median longitudinal fracture extends to or beyond the posterior margin of the sixth abdominal segment (ANTHRENINAE; TRINODINAE, part). 10.
- 2. Abdomen with only five gin-traps, the first of which is on segments 2-3; posterior jaws of gin-traps finely and densely tuberculate. Middle dorsal surface of thorax and abdomen with numerous large and heavily sclerotised tubercles (DERMESTINAE) 3.
- Abdomen with six gin-traps, the first of which is on segments 1-2; posterior jaw of gin-traps knife-like and without tubercles (*Attagenus*) 7.
- 3. Anterior jaws of gin-traps finely but very distinctly toothed 4.
- Anterior jaws of gin-traps not toothed but with scarcely visible (mag. $\times 75$) tubercles on their posterior margins (fig. 13) 6.
- 4. Metathorax without an oval depression near middle anterior margin (jaws of gin-traps as in *D. peruvianus* described below) *Dermestes carnivorus* Fabricius.
- Metathorax near middle anterior margin with an oval depression which is as broad (*D. peruvianus*) to three or more times as broad (*D. lardarius*) as one of the coarse tubercles and has its posterior margin feebly or strongly sclerotised 5.
- 5. Abdomen with a large, broad, transverse, strongly sclerotised tuberculate bar on middle anterior margin of second tergite; anterior jaws of gin-traps very unevenly toothed (fig. 12); posterior jaws straight or only very feebly arcuate with the lateral ends of each not distinctly curved forwards; depression beneath each posterior jaw not distinctly defined at sides. Dorsal surface with tubercles very rarely having an occasional secondary tubercle *Dermestes lardarius* L.
- Abdomen without a distinct sclerotised bar on middle anterior margin of second tergite; anterior jaws of gin-traps very evenly toothed (fig. 11); posterior jaws with their lateral ends distinctly curved forwards; depression beneath each posterior jaw definitely limited at sides. Dorsal surface with tubercles (much coarser and denser than those of *D. lardarius*) of thorax densely studded with conspicuous secondary tubercles (fig. 9) *Dermestes peruvianus* Cast. (S. Amer. form).
- 6. Urogomphi with basal fourth to two-fifths membranous (it is unlikely that this character will serve to distinguish all specimens of *D. maculatus* from *D. ater*). *Dermestes maculatus* Degeer.
- Urogomphi strongly sclerotised from base to apex *Dermestes ater* Degeer.*
- 7. First abdominal tergite with a narrow, sclerotised plate on middle near and parallel to the anterior margin. Dorsal surface densely clothed with very long and fine, golden-testaceous hairs which posteriorly form a dense mat completely covering the seventh to ninth tergites *Attagenus* sp. ? (California, near *piceus* Olivier).
- First abdominal tergite without a sclerotised plate near anterior margin. Dorsal surface less densely clothed with shorter hairs which do not form a very distinct mat over the seventh to ninth tergites. 8.
- 8. Urogomphi (cerci) somewhat abruptly narrowed at about apical two-fifths; proximal half scarcely sclerotised, apical half very strongly sclerotised. Eighth and ninth tergites with few hairs as long as or very slightly longer than urogomphi (as compared with the other species of *Attagenus*, the hairs of the whole dorsal surface are coarser, shorter, sparser, and more erect) *Attagenus gloriosae* Fabricius.
- Urogomphi evenly narrowed from base to apex; base approximately as strongly sclerotised as apex. Eighth and ninth tergites with nearly all hairs very much longer than urogomphi. 9.
- 9. Posterior sclerotised plates (anterior jaws of gin-traps) of first five tergites

- with 44-52 teeth (fig. 18) and strongly declivous immediately before toothed margin; surface of these plates smooth between coarse punctures or only with an occasional microscopic puncture (this character is best seen in dry specimens) *Attagenus pellio* (L.).
- . Posterior sclerotised plates of first five tergites with 27-34 teeth (fig. 17) and not or scarcely noticeably declivous immediately before anterior margin; surface of these plates with numerous distinct microscopic punctures between coarse punctures *Attagenus schäfferi* (Herbst).
10. Abdomen with three gin-traps on segments 1-2, 2-3, and 3-4 11.
- . Abdomen without gin-traps 13.
11. Posterior jaw of each gin-trap with a single row of acute teeth; depression beneath posterior jaw with a sclerotised and conspicuous transverse ridge before anterior margin of segment *Anthrenocerus australis* (Hope).
- . Posterior jaw of each gin-trap with numerous acute tubercles arranged in two or three rows (fig. 19); depression beneath posterior jaw without a sclerotised transverse ridge 12.
12. Posterior margin of fourth abdominal tergite broadly and strongly sclerotised *Trogoderma megatomoides* Reitter.
- . Posterior margin of fourth abdominal tergite at most narrowly, feebly, and indistinctly sclerotised *Trogoderma versicolor* (Creutzer).
13. Abdomen with posterior margin of first three segments narrowly but very distinctly sclerotised *Anthrenus vorax* Waterhouse.
- . Abdomen with posterior margins of first three tergites not or scarcely noticeably (mag. $\times 75$) sclerotised *Anthrenus verbasci* (L.).

In addition to the species included in the key, the following pupae, all without gin-traps, were also examined:—

TRINODINAE: *Trinodes hirtus* (F.).*

ANTHRENINAE: *Megatoma undata* (L.)*; *Thaumaglossa bimaculata* Arrow*; *T. hilleri* Reitter*; *Anthrenus museum* (L.); *A. fuscus* Olivier; and *A. coloratus* Reitter.*

2. PTILODACTYLIDAE.

The pupa of *Anchytarsus bicolor* Melsheimer has been figured by Bertrand (1939: fig. 10). It has dorsal median gin-traps on segments 1-2, 2-3, 3-4, 4-5, and 5-6. According to Bertrand's figure, the middle posterior margin of the sixth abdominal tergite is heavily sclerotised, but there appears to be no sclerotisation on the anterior margin of the seventh tergite.

Three undetermined species of *Ptilodactyla* Illiger have been examined, two from Costa Rica and one from Brazil. These differ very considerably from *Anchytarsus* Guérin-Ménéville. Each has only one gin-trap, which is on segments 1-2 (fig. 20). In all three species there are four very long, thick, secondarily spinose setae on the pronotum, one near each of the anterior and posterior angles. In *Anchytarsus* there are only two similar setae, one on each side near the postero-lateral angle.

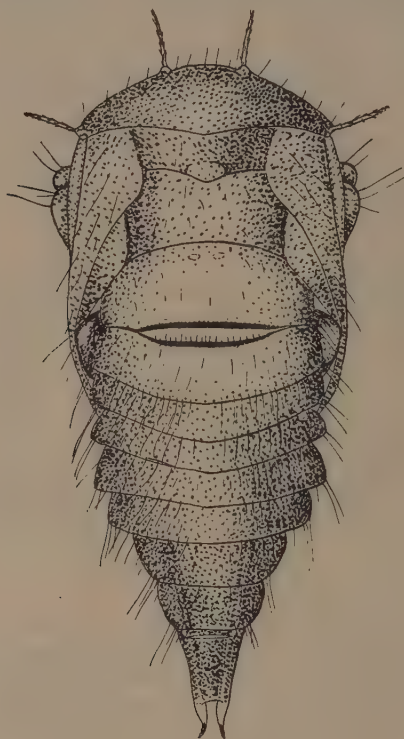
The first two abdominal segments of *Ptilodactyla* are strongly convex, so that from a dorsal view the area around the gin-trap is the highest part of the body. The anterior and posterior jaws of the gin-trap are nearly straight, and the margins of both are smooth. The posterior jaw slides under the anterior jaw when the trap is closed. Immediately beneath the posterior jaw is a single row of long setae which are directed downwards and towards the intersegmental line.

Very little indeed is known of the biology of the PTILODACTYLIDAE, but it

appears that the larvae usually pupate in cells in the earth or in rotten wood. The cuticle of the last larval instar is completely shed by the pupa.

3. DRYOPIDAE.

I have been able to examine only the pupa of *Dryops luridus* Erichson (figs. 21-23). This species has five median gin-traps on segments 2-3, 3-4, 4-5, 5-6, and 6-7. When these are closed the anterior jaw fits under the posterior,



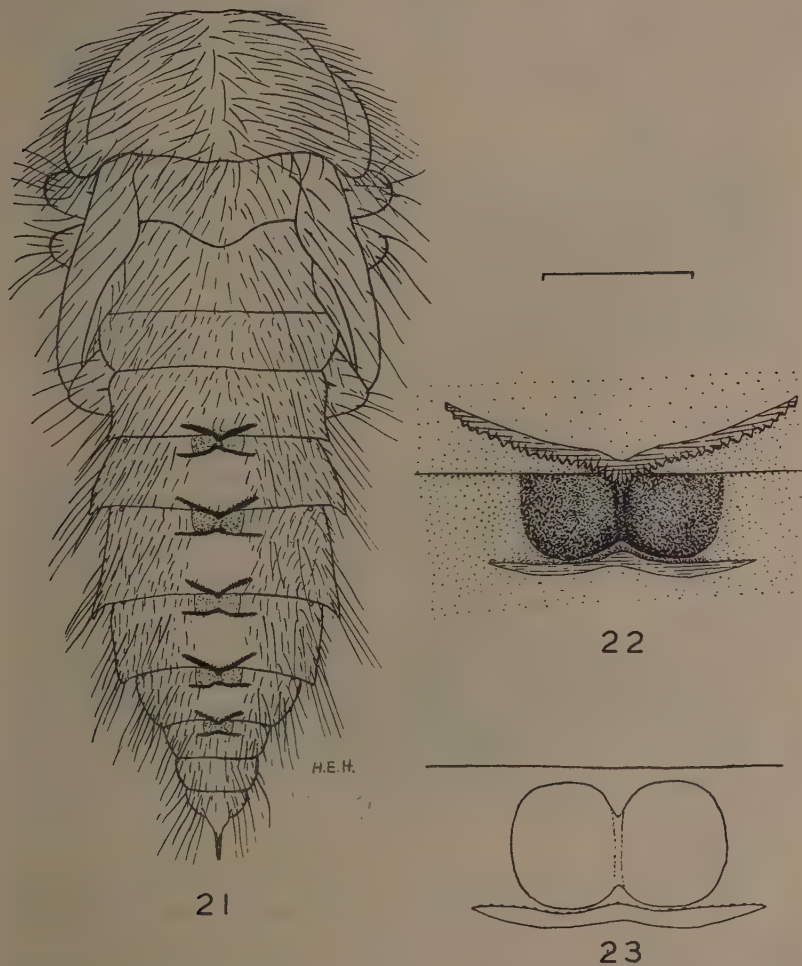
20

FIG. 20.—*Ptilodactyla* sp. from Nova Teutonia, Brazil.

and not the other way around as in the DERMESTIDAE and PTILODACTYLIDAE. The depression beneath the jaws is very sharply defined and is confined to the segment that bears the posterior jaw. The depression (figs. 22-23) consists of two large oval areas separated by a low, narrow, median longitudinal ridge which at either end joins a short ledge-like projection. When the trap is closed, the apex of the anterior jaw rests on the ledge beneath the posterior jaw. The function of the anterior ledge is not clear to me, as when the trap is closed this ledge is covered by the posterior part of the segment bearing the anterior jaw.

Beling (1882) has described the pupa of *Helichus substriatus* Muller, and Bertrand (1939) has described and figured the pupae of *Dryops auriculatus*

Fourcroy, *D. ernesti* Gozis and that of an undetermined species. From their descriptions and figures it is clear that these other species of the family are structurally very similar to *Dryops luridus*. The species of *Dryops* Olivier apparently differ mainly in the way in which the anterior jaw is toothed.



FIGS. 21-23.—*Dryops luridus* Erichson. (21) Dorsal view of pupa. (22) Third gin-trap. (23) Outline of depression of same on fifth abdominal tergite.

The larvae of the DRYOPIDAE usually live in damp places and some, e.g. *Dryops luridus*, are also able to live under water. They pupate in cells in the earth or in rotten wood, and the pupa completely sheds the last larval cuticle.

B. Paired median gin-traps.

Paired median gin-traps have so far been found only in the SCARABAEIDAE (DYNASTINAE) and CERAMBYCIDAE (PRIONINAE). Their basic structure is the same as that of the single median organs of other families. The two gin-traps constituting each pair formed by modifications of the same two abdominal segments open and close simultaneously. Each pair is narrowly separated on the dorso-median line of the abdomen, and each gin-trap is some distance from the sides of the abdomen.

1. SCARABAEIDAE.

Pupae of the COPRINAE, MELOLONTHINAE, DYNASTINAE, and CETONIINAE were examined, but gin-traps were only found in the DYNASTINAE. The extent of their occurrence in this subfamily is unknown, as species belonging to only three genera (*Dynastes* Kirby, *Oryctes* Illiger, and *Chalcosoma* Hope) were available. Of these, all have gin-traps on segments 1-2, 2-3, 3-4, 4-5, and 5-6, and *Dynastes* (*D. gideon* L.) has, in addition, a less well-developed pair on segments 6-7. The gin-traps of these three genera of DYNASTINAE resemble those of some of the PRIONINAE (fig. 25) remarkably closely, and in both groups the posterior jaw slides over the anterior jaw when the traps are closed.

2. CERAMBYCIDAE.

Gin-traps are present in some PRIONINAE, but they appear to be absent in the CERAMBYCINAE and LAMIINAE, judging from the fair number of figures and specimens examined. The PRIONINAE are without doubt the most primitive Cerambycids. The occurrence of gin-traps in this subfamily is most erratic. These structures are lacking in the primitive Paranderini and also in the Prionini (*Prionus*), the latter group possibly being the most specialised in the subfamily. Gin-traps are present in all the Macrotonini seen (5 genera, 6 species) but are absent in one of the two genera of Callipogonini examined.

Of the Callipogonini which have been seen, *Megopis* (*Dandamis*) *nigropunctatus* Arrow has none, but in both species of *Ergates* Audinet-Serville gin-traps are well developed. *Ergates faber* L. (fig. 25) has these structures on segments 2-3, 3-4, 4-5, 5-6, and 6-7. Those on segments 6-7 are distinct but much less developed than the more anterior traps. *E. spiculatus* Leconte has gin-traps only on segments 2-3, 3-4, 4-5, and 5-6; and the anterior margin of the posterior jaw of each is very strongly toothed instead of smooth as in *E. faber* L. (fig. 25).

In the Macrotonini two very distinct kinds of paired median gin-traps occur. The usual kind is exactly like that of the Callipogonini (fig. 25), and it is the kind possessed by *Stenodontes damicornis* L., *Mallodon maxillosus* Drury, *Olethrius insularis* Fairmaire, and *Macrotona* sp. (from Kenya). It may be called the cup type to distinguish it from the tuberculate type (fig. 24), which I have only found in *Macrotona serripes* Fabricius and an unidentified genus and species from Spanish Guinea.

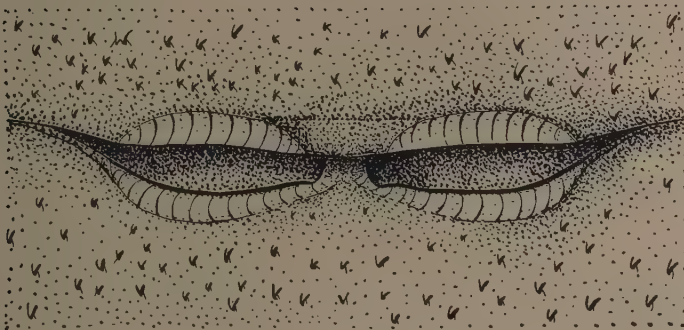
The tuberculate type of the Macrotonini is present only on segments 3-4, 4-5, and 5-6, whereas the cup type is present on segments 2-3, 3-4, 4-5, 5-6, and 6-7 except in *Olethrius* Thomson, where they are absent on 6-7. In the latter genus there is a very feebly developed trap on segments 1-2.

The way in which the two kinds of traps close is very different. When the

abdomen is bent upwards, the posterior jaw of the cup type slides over the anterior jaw. The tubercle-like anterior jaw of the tuberculate type is directed upwards at an angle of about 45 degrees from the horizontal axis of the body. In this type the first upward movement of the abdomen has the effect of pressing in the part of the segment between and below the anterior jaws, so that these



24



25

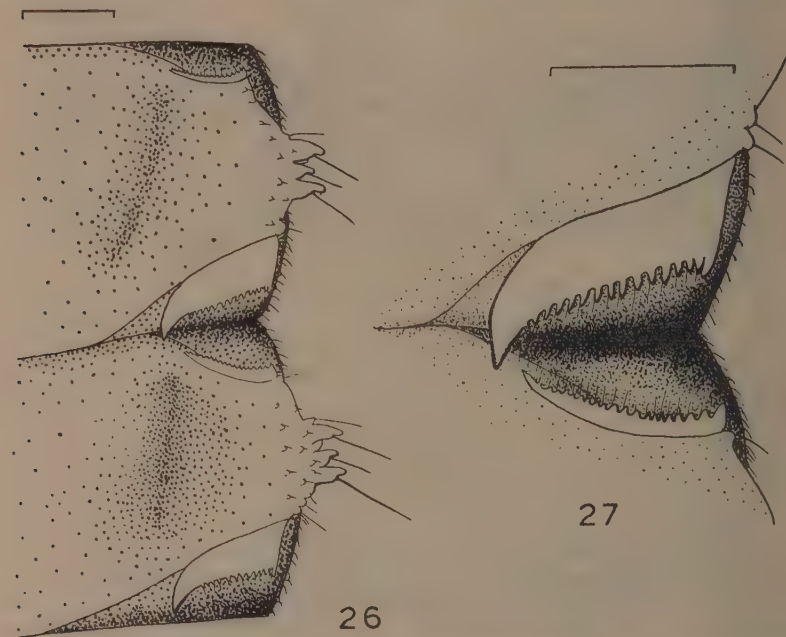
FIGS. 24-25.—(24) Third gin-trap of *Macrotoma serripes* F. (25) Fourth gin-trap of *Ergates faber* L.

are necessarily deflected downwards. This action is so synchronised that when the abdomen is bent upwards to its maximum extent and the trap is closed, the anterior jaw is nearly horizontal and has been partially enclosed by the concave posterior jaw which has moved forwards. When the trap is closed, the apex or point of the anterior jaw rests in the deepest part of the concavity

of the posterior jaw. The inner or median margin of both jaws, when seen from the side, grind together in a scissor-like fashion with the median margin of the posterior jaw dorsad to the median margin of the anterior jaw. This description of the closing of the jaws of the Macrotomini is based on manipulation of preserved specimens, no living examples being available.

III. LATERAL GIN-TRAPS.

Lateral gin-traps have been found only in some of the pupae of the family TENEBRIONIDAE. As the pupae of only 15 species have been seen, no general-



FIGS. 26-27.—*Alphitobius diaperinus* Panzer. (26) Second gin-trap. (27) Enlarged view of same.

isations as to the occurrence of these structures in the family, one of the most extensive among beetles, can profitably be made. The jaws of the lateral gin-traps (figs. 26-27) are borne on projecting lateral flanges of the segments so that between each pair is a considerable drop which serves the function of the depression between the jaws of the single and paired median organs.

Gin-traps occur in the genera *Tribolium* Macleay, *Tenebrio* L., *Gnathocerus* Thunberg, *Alphitobius* Stephens, *Anthracias* Redtenbacher, gen. indet., and probably very many others. Of the eight genera examined, they were lacking in *Pycnocerus* Westwood and *Catamergus* Fairmaire. Species possessing gin-traps always had five or six pairs on segments 1-2, 2-3, 3-4, 4-5, and 5-6 or on these plus segments 6-7. The jaws are strongly sclerotised and toothed or serrate, and they possess good generic and specific characters. When the traps are closed, the posterior jaw always slides under the anterior jaw. The movements

of the abdomen that close the lateral gin-traps are different from those that close the median traps. These differences in movement are not due to differences in the position of the two chief kinds of gin-traps, but are primary and cause the development of these structures in their particular positions.

IV. DISCUSSION.

Until now no direct evidence has been produced for the claim that the gin-traps are pinching organs which serve to protect the pupae from their enemies. The indirect evidence I have already discussed, considered with the results of a few preliminary experiments, described below, would appear to establish beyond dispute the fact that the gin-traps are structures which do protect the pupae by pinching their enemies. A number of objections may be made to this claim. The more rational of these are that the gin-traps are structures for stridulation, or for locomotion, or for attachment to the pupal cell, or, finally, that they are of no direct significance, but that their occurrence and varied structure is only incidental or fortuitous and the result of selection acting on physiological or other characters to which they are linked. Most of these objections are easily disposed of as shown below.

Stridulating organs may develop in insects wherever two sclerotised parts rub or can be made to rub against each other. Although their location is diverse, their fundamental structure is not. Each consists of a file-like area on one sclerite and a point or tubercle, commonly a series of tubercles, on another sclerite or appendage. The tuberculate area is rasped across the file-like or ridged area to produce sound. Such stridulatory organs occur in all beetles which stridulate at frequencies audible to the unaided human ear. Organs essentially identical to these have been detected in some beetles (weevils and Cerambycids) which do not produce an audible sound, but it is assumed in these instances that sound at frequencies inaudible to humans is nevertheless produced. It may also be true that sound at very high frequencies is produced by very fine structures not yet recognised.

So far as the gin-traps are concerned, it is clear that they are not sound-producing organs or at least sound-producing organs of any recognised kind. The morphological basis for a sound-producing organ is lacking in all gin-traps except possibly only in those of *Dermestes maculatus* Degeer, where the anterior jaw of each trap is tuberculate so that when the trap is closed these tubercles rub against those of the posterior jaw. Owing to the size and spacing of the tubercles, it would seem that if sound is produced it should be at a frequency low enough to be audible to humans, which is not the case. Furthermore, the structure is atypical in the sense of having tubercles rubbing against tubercles instead of tubercles rubbing against ridges or files. While there is nothing inherently impossible in the gin-traps having a dual function—pinching and producing sound—it does appear that if there is any sound produced the modifications necessary to produce it are secondary and of all the forms examined present only in *D. maculatus* Degeer.

With the possible exception of the PRIONINAE, of which I have had no living examples, the pupae that possess gin-traps move only to a very limited extent by violent wriggles; and such changes in position as may occur are not aided by the gin-traps. The gin-traps can hardly be locomotor organs, as they do not come in contact with the substrate except in the Macrotomini and TENEBRIONIDAE. In the Macrotomini, the movement of the abdomen necessary to close the gin-traps results in these organs sinking between their respective

segments so that they are unable to obtain a purchase on the substrate. This is true, regardless of the position in which the pupa may be lying.

Many of the TENEBRIONIDAE such as *Tenebrio* L. and *Tribolium* Macleay pupate on the surface of their food and often lie on their dorsal or ventral surfaces. In such positions the gin-traps are freely exposed and obviously cannot obtain the friction necessary for locomotion. But these pupae also often rest on their sides in such a way that the gin-traps along one side may be in contact with the cereal or other food owing to the fact that the lateral flanges may be partly sunk below the surface of the food. Pupae made to wriggle in this position do not, however, progress in any direction.

Pupae of *Tenebrio* and *Tribolium* are often eaten by larvae of their own species when the relative humidity or moisture content of the food is low. The larvae apparently always migrate to the surface before pupation. An explanation of this habit may be that pupae at the surface are less liable to attack by larvae of their own or other species. When forced to pupate beneath the surface, the larvae do not construct a definite pupal cell and the gin-traps of the pupae are partly obstructed by the food and therefore presumably less efficient. It might be imagined that it would be of some advantage to the pupae to be able to wriggle to the surface when for one reason or another they were covered by the cereal or other food. Pupae of *Tenebrio molitor* L. were buried at depths of 10, 20, 30, and 50 mm. in coarse oatmeal, but in each case the pupa remained where it had been buried until the adult emerged. Since beetles always shed their pupal cuticle before emerging from their pupal cells, the gin-traps of the PTILODACTYLIDAE, DRYOPIDAE, DYNASTINAE, and such DERMESTIDAE as possess pupal cells can hardly be locomotor organs quite apart from the other reasons already given.

It might be argued that the gin-traps are organs for attachment of the pupa to the pupal cell. That this is not the case is shown by the fact that so many of the pupae possessing well-developed gin-traps have no pupal cells, as well as by the fact that in those which do possess pupal cells the gin-traps do not come into contact with the cell walls except in the Macrotomini. In all cases where the pupa is known to be attached to the pupal cell (some Neuroptera (?), a few aquatic Diptera, many Lepidoptera), at least the inner surface of the pupal cell is silk, and spines which project out from the surface of the body are entangled in the silken strands.

On the body of nearly all insects there are ridges, spines, and various kinds of structures of unknown function. It is also common to find that closely related insects which have established what appear to be identical relations with exactly similar physical and biological environments nevertheless differ strikingly as regards their external features—the number or shape of various setae, spines, or other processes. The great difficulty or impossibility of providing satisfactory experimental proof of the selective value and function of the bewildering variety of such structures accounts in part for the popularity of theories which over-emphasise the non-selective nature of minor external features. Broadly speaking, those who hold such theories claim that these structures are linked to quite different attributes, perhaps physiological, and the variations that they exhibit are fortuitous in the sense that they result from the selection of the totally different characters to which they are linked. That this is so in some instances is well known. A relation of this sort may exist between any two parts which are allometrically related. To admit that relationships of this type sometimes exist and produce fortuitous variations of structure is very different indeed from assuming that all structures the

function or selective value of which is unknown are fortuitous. Another argument often produced in support of the non-selective nature of minor external features owes its origin to the fact that it is difficult to believe that animals are so intimately related to their environment—fit so tightly—that the minute differences to be seen between related species have selective value. But variations of structure relatively insignificant over short periods of time can be supposed to have an important selective effect where many thousands of generations are concerned. These theories no doubt owe some of their popularity to a reaction against many of the naïve and subjective explanations of the use or selective value of variations of colour and number or shape of spines and other processes as well as to the general absence of experimental evidence.

The relatively complex structure of the gin-traps and the fact that they are used to pinch enemies which attack the pupae are sufficient to show that they are not fortuitous in the sense in which this term is used in the preceding paragraph.

In the following paragraphs the results of a few experiments are recorded. Two species were used, *Dermestes maculatus* Degeer with unpaired median gin-traps and *Tenebrio molitor* L. with lateral gin-traps. The sole object of the experiments was to discover if the gin-traps were used to protect the pupae by pinching their enemies. As soon as it was established beyond question that the gin-traps did afford some protection to the pupae, the experiments were discontinued. No distinction was made between the pupa and the pharate (Hinton, 1946a) phase of the adult. Both instars use the pupal gin-traps in the same, or approximately the same, manner.

A number of *Dermestes* pupae were confined with larvae of the same species and adults of *Necrobia rufipes* Degeer. Under natural conditions the pupae are known to be eaten by larvae of their own species as well as by adults of *Necrobia rufipes*. When *Dermestes* or *Necrobia* Olivier touched or crawled on the pupae, one or more of the gin-traps were closed and opened, and this opening and closing of the gin-traps was sometimes continued for a few seconds after the larva or adult had left the pupa. The larvae and adults often had their tarsi momentarily pinched by a gin-trap. When pinched they would at once leave the pupa. The fact that the pupae are sometimes eaten by these larvae and adults is proof that the gin-traps do not entirely protect the pupae.

Owing to the difficulty of observing exactly what occurs when *Necrobia* adults and *Dermestes* larvae attack or accidentally crawl on the pupae—*Necrobia* moves too fast and *Dermestes* is too hairy—a search was made for a small and slow-moving animal that would attack the pupae. A Thrombiculid mite, *Allothrombium fuliginosum* Hermann, was found to be ideal for this purpose.

A pupa was placed in a solid watch-glass with five mites. The watch-glass was covered with a glass slide and the attacks of the mites were observed under a binocular at a magnification of $\times 75$. This experiment was repeated with three other pupae and fresh lots of mites. The length ratio of the mite to the pupa is approximately 2.5 : 6–9 mm. More than 50 different attacks by mites on pupae were observed.

The mites were unable to feed on the dorsal or lateral parts of the abdomen except sometimes for very short periods. When they began to bite, the gin-traps were rapidly closed and opened, and, as several legs were on the dorsum, in all cases one or the other was soon pinched and the mite ran away. When a leg was pinched, no permanent injury appeared to be inflicted, judging from

the way the leg was used after its release and by the fact that after a short interval the mite that was pinched would often return to the attack. If the pupa was lying on its dorsum, the mites often attacked its ventral surface. In all such cases observed the violent wriggles of the pupa caused it to roll over on the mite in a few seconds, when the mite always ran away. If the pupa was lying on its ventral surface, attacks on the dorsum of the thorax were eventually repelled by rolling over on the mite if the legs of the mite were so placed that they were out of reach of the gin-traps. The mite was, however, able to feed more or less uninterruptedly on the head and extreme caudal end between the urogomphi. In both positions the legs of the mite were out of reach of the gin-traps, and the pupa was unable to roll on the mite.

When the pupa is strongly stimulated all the gin-traps are closed and opened more or less simultaneously, and the end of the pupa describes a narrow ellipse with the long axis vertical. But when the stimulation is slight and localised any one of the five gin-traps can be snapped shut independently of all others. Experiments with *Tenebrio molitor* L. showed that it can also close any one of its six gin-traps independently of all others. Pupae of the latter species were enclosed in petri dishes with larvae of their own species, larvae of *Dermestes maculatus* Degeer, and adults of *Necrobia rufipes* Degeer; and it was clear that the gin-traps served to protect the pupae. One of the most noticeable differences in behaviour between the pupae of *Dermestes* and *Tenebrio* was that the larvae and adults could generally crawl freely over *Tenebrio* pupae without eliciting a response, and in most cases the pupae would only snap their gin-traps when they began to be bitten. In *Dermestes*, on the other hand, the gin-traps were usually brought into play as soon as the larvae or adults crawled on the pupae.

In all cases observed the gin-traps of *Tenebrio* and *Dermestes* did not remain closed for more than a very short time. They were usually snapped shut for only a fraction of a second. It does not appear unreasonable to suppose that if the gin-traps remained closed for any length of time while they held a predator, the attempts of the latter to free itself would often result in serious injury to the pupa.

POSTSCRIPT.

While this paper was in the press I found an interesting observation on gin-traps by Gravely (1915). This writer has heard the pupa of *Oryctes rhinoceros* L. stridulate, and he has described as stridulatory organs the structures I have called gin-traps. Further study of preserved pupae of a species of *Oryctes* and the closely related genus *Dynastes* (*D. gideon* L.) has revealed some most interesting facts. The jaws of the gin-traps of *D. gideon* are microscopically punctate but have no trace of ridges or tubercles, and when mechanically manipulated do not produce any audible vibrations. However, when the abdomen of a specimen in the late pharate adult phase is moved up and down, a faint but distinct stridulation is produced in a most curious way. As is well known, the adult stridulates by rubbing the seventh abdominal tergite, which is transversely ridged, against the tips of the elytra. In the late pharate adult phase the imaginal cuticle is fairly hard and the pupal cuticle fairly loosely attached and somewhat displaced. When the abdomen is moved, the inner and heavily sclerotised ridge between the sixth and seventh segments of the pupa is moved over the transversely ridged seventh tergite of the adult to produce the stridulation.

Mechanical manipulation of the abdomen of *Oryctes* in a late, but not in an

early, pharate adult phase also produces audible vibrations in an exactly similar manner. But *Oryctes* also stridulates in another way. The dorsal part of the pupal cuticle was removed and manipulated separately, and there was no doubt that the gin-traps could stridulate. This stridulation is produced by the lower edge of the posterior jaw moving over the obliquely ridged upper surface of the anterior jaw, and the frequency of the vibrations thus produced is not the same as that produced when the pupal cuticle is rubbed over the seventh abdominal tergite of the adult.

Although it can definitely be said that in the genus *Oryctes* the gin-traps are slightly modified to enable them to stridulate, it will be clear from the general account of the gin-traps already given that the modifications necessary to stridulate can only be regarded as secondary. This belief is strongly supported by the fact that in the closely related *Dynastes* the gin-traps are unable to stridulate.

Gravely (1915 : 498) records gin-traps in *Adoretus* Laporte (SCARABAEIDAE, RUTELINAE) and in *Hectarthrum* Newman (CUCUJIDAE), but says that in neither genus do these structures appear to be capable of stridulating. I have been unable to examine pupae of *Hectarthrum*, but those of *Adoretus versutus* Harold and *A. punctipennis* Fähræus have six well-developed gin-traps on segments 1-2, 2-3, 3-4, 4-5, 5-6, and 6-7. The jaws of these gin-traps are smooth and obviously incapable of stridulating.

I have recently (October, 1946) found that gin-traps are present in the pupae of some PSEPHENIDAE. An undetermined species of *Eubria* Latreille (or closely allied genus) from Tasmania has paired median gin-traps on segments 2-3, 3-4, 4-5, 5-6, and 6-7. Unlike those of the SCARABAEIDAE and CERAMBYCIDAE, these are widely separated on the middle of the body, and the posterior jaws move under the anterior jaws. The posterior jaws are moderately coarsely tuberculate and the anterior jaws are very densely and microscopically tuberculate.

The distribution of the various kinds of gin-traps is as follows :—

I. Median Gin-traps.

A. Single.

DERMESTIDAE (most).

PTILODACTYLIDAE (*Anchytarsus*, *Ptilodactyla*).

DRYOPIDAE (*Dryops*, *Helichus*).

B. Paired.

SCARABAEIDAE (DYNASTINAE, some RUTELINAE).

PSEPHENIDAE (some EUBRIINAE).

CUCUJIDAE (*Hectarthrum*).

CERAMBYCIDAE (some PRIONINAE).

II. Lateral Gin-traps.

TENEBRIONIDAE (many).

ACKNOWLEDGMENTS.

My best thanks are due to Professor G. D. Hale Carpenter for the interest he has taken in this paper and for the valuable suggestions he has made. My thanks are also due to Dr. F. van Emden for the pupae of three species of PTILODACTYLIDAE.

REFERENCES.

- BELING, T., 1882, Beitrag zur Biologie einiger Käfer aus den Familien DASYLLIDAE und PARNIDAE. *Verh. zool.-bot. Ges. Wien* **32**: 435-42.
- BERTRAND, H., 1939, Les larves et nymphes des Dryopides Palearctiques. *Ann. Sci. nat. (Zool.)* **11**: 299-412, 216 figs.
- GRAVELY, F. H., 1915, Notes on the habits of Indian insects, myriapods and arachnids. *Rec. Indian Mus.* **11**: 483-539, 4 pls.
- HINTON, H. E., 1945, *A monograph of the beetles associated with stored products* **1**: 443 pp., 505 figs. London.
- , 1946a, Concealed phases in the metamorphosis of insects. *Nature* **157**: 552-3, 1 fig.
- , 1946b, A new classification of insect pupae. *Proc. zool. Soc. Lond.* **116**: 282-328, 64 figs.
- NORRIS, M. J., 1936, Experiments on some factors affecting fertility in *Trogoderma versicolor* Creutz. (Coleoptera, DERMESTIDAE). *J. anim. Ecol.* **5**: 19-22.

Vol. 97. Part 20. Pp. 497-583, 75 figs.*

23rd December, 1946.

THE
TRANSACTIONS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

MP. INST. ENT.
LIBRARY
30 DEC 1946
Em. 344

World List abbreviation: Trans. R. ent. Soc. Lond.

CONTENTS

PAGE

X HALL, W. J., D.Sc., F.R.E.S. On the Ethiopian
Diaspidini (Coccoidea) 497-583, 75 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price £1 10s. 0d.

* With title-page, contents and index.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING:

OFFICERS and COUNCIL for the SESSION, 1946–1947.

PROF. G. D. HALE CARPENTER, M.B.E., D.M., *President*.

W. J. HALL, D.Sc.	} <i>Vice-Presidents</i> .
C. B. WILLIAMS, M.A., D.Sc.	
H. B. WILLIAMS, LL.D.	

A. WELTI, *Treasurer*.

N. D. RILEY, *Secretary*.

Other Members of Council.

C. H. ANDREWES, F.R.S.	CAPT. R. A. JACKSON, R.N.
J. W. EVANS, M.A., D.Sc.	MISS C. E. LONGFIELD.
G. FOX-WILSON, N.D.H.	SIR GUY A. K. MARSHALL, K.C.M.G.,
R. M. GREENSLADE.	D.Sc., F.R.S.
FRANCIS HEMMING, C.M.G., C.B.E.	G. E. J. NIXON, B.A.
H. E. HINTON, B.Sc., PH.D.	J. F. PERKINS, B.Sc.

Finance and House Committee.

G. FOX-WILSON, N.D.H. (*Chairman*).

J. W. EVANS, M.A., D.Sc.	W. RAIT-SMITH.
FRANCIS HEMMING, C.M.G., C.B.E.	O. W. RICHARDS, M.A., D.Sc.
H. E. HINTON, B.Sc., PH.D.	

Publication and Library Committee.

W. J. HALL, D.Sc. (*Chairman*).

H. E. HINTON, B.Sc., PH.D.	J. SMART, B.Sc., PH.D.
B. M. HOBBY, M.A., D.PHIL.	W. H. THORPE, M.A., Sc.D.
J. F. PERKINS, B.Sc.	

Committee on Generic Nomenclature.

FRANCIS HEMMING, C.M.G., C.B.E. (*Chairman*).

W. A. F. BALFOUR-BROWNE, F.R.S.E.	O. W. RICHARDS, M.A., D.Sc.
K. G. BLAIR, D.Sc.	N. D. RILEY (<i>Secretary</i>).

Committee for the Protection of British Insects.

H. M. EDELSTEN, O.B.E. (*Chairman*).

R. B. BENSON, M.A.	A. M. MASSEE, D.Sc.
E. A. COCKAYNE, M.A., M.D., F.R.C.P.	THE HON. MIRIAM ROTHSCHILD.
CAPT. R. A. JACKSON, R.N.	W. H. THORPE, M.A., Sc.D.
COL. F. A. LABOUCHERE.	N. D. RILEY (<i>Secretary</i>).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

- 1. British National Committee for Biology** (Royal Society).
Mr. Francis Hemming, C.M.G., C.B.E., appointed 1946.
Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.
- 2. Local Committee of Management of Wicken Fen.**
Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].
- 3. National Trust for Places of Historic Interest or Natural Beauty.**
Mr. H. M. Edelsten, O.B.E., appointed 1944.
- 4. New Forest Association.**
Mr. W. Fassnidge, appointed 1934.
- 5. New Forest Joint Committee.**
Mr. W. Fassnidge, appointed 1939. *Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.*
- 6. Royal Meteorological Society. Phenological Committee.**
Dr. C. B. Williams, M.A., D.Sc., appointed 1937.
- 7. Council for the Promotion of Field Studies.**
Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.
- 8. Joint Bioclimatic Committee.**
Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
Dr. C. B. Williams, M.A., D.Sc., appointed 1945.
- 9. Yorkshire Naturalists' Trust Ltd.**
Mr. W. D. Hucks, M.P.S., appointed 1946.

ON THE ETHIOPIAN DIASPIDINI (COCCOIDEA)

By W. J. HALL, D.Sc., F.R.E.S.

(Imperial Institute of Entomology.)

Manuscript received 7th May, 1946.

(Read 2nd October, 1946.)

WITH 75 TEXT-FIGURES.

SOME 200 species belonging to genera of the tribe Diaspidini have been described or recorded from the Ethiopian region, *i.e.* the whole of the African continent south of the Sahara. Apart from a monograph by Brain on the COCCIDÆ of South Africa (1915-20), these records have appeared in a wide variety of scientific journals in papers contributed by several authors, notably Newstead, Lindinger, Leonardi, Malenotti, Laing, Vayssi  re and the present author.

The African continent is so vast that there are still large areas that are very imperfectly known and very much larger areas that have never been searched for Coccids. This is hardly surprising when it is remembered that, prior to 1890, only a handful of explorers and missionaries had penetrated into the interior, and knowledge of the continent was largely confined to parts of the seaboard and the vicinity of the ports. Many of the earlier records, therefore, were of known species that had probably been introduced, and it was not until the interior began to become better known, and development to take place, that the wealth of Coccid species both old and new began to reveal itself. Up to the present day it is only in the Union of South Africa, Southern Rhodesia and Uganda that systematic collecting on a limited scale has been carried out, and this is reflected by the fact that 115 out of the 200 species recorded have been found in these three territories; from many of the countries there are surprisingly few records. Even in the three territories mentioned there can be little doubt, in view of their size, that very many species remain to be found, so it is quite certain that the 200 Diaspidine species so far recorded represent but a small percentage of the number actually present.

Extremely conservative generic conceptions prevailed amongst most of those who worked on the Ethiopian fauna up to 25 years ago, and then, in 1921, MacGillivray published his COCCIDÆ of the World, revolutionising the classification of the Coccoidea, and of the DIASPIDIDÆ in particular. In view of the conservatism of earlier workers, MacGillivray was on relatively safe ground when he erected a very large number of new genera. Unfortunately, however, he often failed to understand either the old-established genera, or even those that he created himself, with the result that his grouping of species was, in many instances, quite wrong and meaningless. It is perhaps fortunate that only one-half of the 200 Ethiopian species now known had been recorded when MacGillivray published his work. Ferris has cleared up much of the confusion which resulted from MacGillivray's work by publishing admirable drawings of the type species of genera (including many of MacGillivray's genera) in *Microentomology*, and in his *Atlas of the Scale Insects of North America*. The

value of these works as a contribution to the study of this group of insects cannot be over-estimated, but only a limited number of the species recorded from the Ethiopian region and of MacGillivray's Ethiopian genera have been available to Ferris in the course of these studies.

Whilst Ferris and, to a lesser degree, McKenzie were clearing up the confusion to which MacGillivray's work had given rise, Lindinger (1937: 178) published a list of the genera of Coccoidea that made the confusion created by MacGillivray even more chaotic. This list included a considerable amount of synonymy of the genera of Diaspidini by which many well-known genera were sunk and many others, including several of MacGillivray's genera, were fused without any apparently valid grounds. So far as the Ethiopian genera are concerned, the synonymy proposed has been disregarded except in one or two instances.

The types or either typical, or what is believed to be typical, material of over 80% of all the species recorded have been available to the author, and it is felt that this justifies an attempt to reduce them to some sort of order, and to provide a framework into which the species remaining to be found can be fitted.¹ The present paper has been based on the examination of this authentic material and in particular on genotypes. Many of MacGillivray's genera have been accepted in this work and, in addition, it has been found necessary to create several new genera. The latter course has only been adopted with the greatest reluctance, but in the present state of our knowledge it is not possible to assign the species concerned to any of the known genera. Of the thirteen new genera created seven are at the moment monotypical, but as the fauna becomes better known no doubt other species referable to them will be found. This view is strengthened by the knowledge that MacGillivray erected the genus *Afriaspis* with only two included species—which have since been shown to be synonymous—yet eleven species have been referred to it in the present paper and it is now recognised as a well-established genus; the same applies to other genera erected by this author. Nevertheless it is realised that, as the number of species increases, gaps between certain genera may be bridged and lead to their fusion.

At least half of the small percentage of species that have not been seen by the author have been species described by Lindinger, chiefly from the Cameroons. This is unfortunate because many of these are very different from anything recorded as yet from elsewhere on the continent. So far as one can judge from our present limited knowledge, the Cameroons is the only area where a specialised fauna, showing marked differences from that of the rest of the continent, exists. It is suspected that this specialised fauna may occur right through the rain-forest area which extends from the Cameroons through French West Equatorial Africa to the northern part of the Belgian Congo. Other areas with a specialised fauna may, of course, come to light later.

One of the characteristics of the Ethiopian fauna is the high development of Chionaspiform species. An indication of this is the fact that not far short of half the total number of species have been recorded, at one time or another, either directly or indirectly as belonging to the genus *Chionaspis* Signoret. Yet, as will be shown below, it is considered extremely doubtful if this genus occurs in the Ethiopian region at all.

¹ The Newstead and Green collections, now incorporated in the National Collection at the Natural History Museum, were also available in the course of the preparation of this paper, through the good offices of Mr. N. D. Riley, Keeper of Entomology, who kindly expedited their return to London after the conclusion of hostilities.

The bulk of these species fall into three main groups.

1. Species in which the median pygidial lobes are widely separated, not yoked basally, often small and frequently smaller than the second lobes. These have been grouped into four genera—*Dentaspis* MacGillivray, *Dentachionaspis* MacGillivray, *Inchoaspis* MacGillivray and *Nelaspis* Hall—which are believed to be typically Ethiopian.

2. Species in which the median lobes are strongly zygotic. The genera *Africaspis* MacGillivray, *Contigaspis* MacGillivray, *Pinnaspis* Cockerell are representative of this group.

3. Species in which the median lobes are not zygotic but separated by a definite notch and yoked together by a basal sclerosis. Many of these in the past have been wrongly assigned to *Phenacaspis* Cooley & Cockerell—an Oriental genus—and three new genera *Rolaspis*, *Tecaspis* and *Voraspis* are erected for the reception of 21 of these species.

It may be remarked that a large number of Ethiopian species exhibit scleroses at the bases of the median lobes, but these are not always completely fused to form a yoke. The shape of the notch between the median lobes, also, may vary from shallow and flatly rounded to acutely V-shaped, but there is no sharp dividing line between a U- and V-notch, and therefore the shape of the notch has not been relied upon as a character of generic significance except where it is definitely linked with other distinguishing features.

Another character that has been observed in some species is a microduct arising from the capitate heads of the marginal macropores. These microducts are not always easy to detect, and in old preparations they are often very obscure. Whilst this is a character that should be looked for, the indications are that, as it is present in some instances in each of the three African genera erected for the "*Phenacaspis*" species, it has no generic importance.

The presence of gland tubercles in a submarginal position on the ventral aspect of the 4th and 5th abdominal segments is another unusual feature which is found in three species of otherwise widely different characters. They are most strongly developed in *Versiculaspis* MacGillivray but have also been noted in *Dentachionaspis* MacGillivray and *Rolaspis* Hall.

Supplementary disc pores anterior to the normal groups of perivulvar pores are a characteristic of the genus *Poliaspis* Maskell. Indications of the presence of such pores are found in many Ethiopian species, and the view is held that a species should not be referred to *Poliaspis* unless it has characters apart from this which make it congeneric with *media* Maskell, the type of the genus. On this basis, not one of the five Ethiopian species is correctly assigned to the genus, and they have been placed in genera with which they are considered to be congeneric on the basis of their other characters despite the presence of the supplementary disc pores.

In the course of the present study the author has been impressed by the fact that resemblances often exist between species that it is difficult to express in terms of key characters. Alternatively, there are species, appearing very similar from the original descriptions and drawings, that, when actually examined, prove to be quite different.

While this paper was in course of preparation, a batch of most excellent and interesting material was received from the Chief Entomologist of the Division of Entomology, Pretoria. This provided new host and locality records for some species, and included as well four new species, the descriptions of which will be found in their appropriate places in this paper.

All the genera known to the author as having been recorded from the

Ethiopian region, with the exception of a few used by Lindinger in his more recent papers on synonymy, are discussed in alphabetical order. MacGillivray in his COCCIDAE of the World neither figured nor described genera, but based their separation on a series of key characters. In all cases where a diagnosis of these genera has not been published by later workers the characters of the genus, as understood by the author, based on part of the type material are given. Figures have been included, where it has been considered necessary, to supplement those already published either by the original author or later workers. Keys for the separation of species are given for all genera containing two or more, but only those species of which either the type, part of the type material or what is believed to be authentic material, are included in these keys.

The detailed discussion of the individual genera is followed by a key for the separation of those genera accepted on the basis of material examined. Every attempt has been made to ensure that the lists of genera and species given at the end of the paper are as complete as possible, and most of the references to literature and distribution are included here. A list of species arranged under their host plants is also given.

The terminology followed is substantially the same as that adopted by Ferris in his *Atlas of the Scale Insects of North America*.

Genus *Adiscoforinia* Leonardi.

Represented by a single species, *A. pygosema* Green & Laing, described from Tanganyika on an unknown host plant. The genus is probably of Oriental origin.

Genus *Africaspis* MacGillivray.

Genotype :—*Diaspis chionaspiformis* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body elongate, pyriform or fusiform. Pygidium with median lobes well developed, close together with at least their inner angles fused (except in one species), without setae, gland spines or marginal pore between the bases of the lobes. Other lobes represented by small dentate projections of the margin. Marginal pores, particularly those of the first two interlobular spaces, heavily sclerotised. Gland spines of the pygidial fringe normally arranged in pairs in the usual positions. Dorsal pores in well-defined segmentally arranged series as far as the 5th segment; on the 6th segment the pores, if present, are usually confined to a few in the submarginal series. Similar pores occur marginally of all segments as far as the mesothorax, and groups of gland tubercles occur in the usual positions. Perivulvar pores normally present in five groups but in one species they are entirely wanting and in another supplementary groups of pores are present in addition to the normal five groups of perivulvar pores. Anal orifice situated towards the base of the pygidium.

Scale of the adult female white, elongate, broadening posteriorly; male scale white, elongate, with more or less parallel sides and usually uncarinated.

Notes.

The genus *Africaspis* is characterised by the nature of the median lobes, the small dentate projections replacing the other lobes and the heavy sclerotisation of the marginal pores of the first two interlobular spaces. It comes closest to *Contigaspis* MacGillivray, a genus in which the median lobes are smaller and which lacks the dentate marginal projections and sclerotisation of the marginal pores. Lindinger (1937:178) placed *Africaspis* as a synonym of *Anoplaspis* Leonardi, a genus to which it bears little or no resemblance at all.

Eleven species are here referred to the genus; most of these have, in the past, been assigned to *Pinnaspis* Cockerell but they are clearly distinct from that genus as at present understood. One species—*parinarii* Hall—was described originally as a *Poliaspis*, attention being drawn at the time to its similarity to *Africaspis chionaspiformis* (Newstead). It has been included here because it has obviously greater affinities with *Africaspis* than *Poliaspis*. At the same time it differs from typical *Africaspis* in having median lobes, although very close together, not fused at their inner angles and with two small setae between them and with gland spines of the pygidial fringe more numerous.

In *caffra* Brain the median lobes appear to be separated, but the sclerotisation at the base of the lobes is such that it is impossible to say whether the inner angles are actually separated or not. This species also differs from the genotype and all other included species in having gland spines of an unusually broad plate-like character.

As a result of the examination of further material of *Chionaspis* (*Pinnaspis*) *communis* var. *monotes* Hall it is considered that this species should be united with *A. chionaspiformis* (Newstead). *Chionaspis cassiae* Newstead has already been synonymised with *chionaspiformis* by Laing (1929: 479). The forms described as *Chionaspis* (*Pinnaspis*) *communis* var. *diospyros* Hall and *C. (P.) communis* var. *berliniae* Hall are believed to be distinct and are here raised to specific rank. *Chionaspis fici* and *berliniae* are very closely allied and further knowledge of the two species may lead to their union, but on the basis of the material at present available they are separable. The same remarks apply also to *chionaspiformis* and *communis*.

The genus *Africaspis* is almost certainly African in origin, and is widely distributed throughout eastern and southern Africa. The genotype is a variable species that is common throughout the whole area and it is fully expected that further collecting will add to the present well-defined group of species. The fact that one species—*pattersoni* Green & Laing—occurs in the Gold Coast suggests that the distribution may eventually be found to be general.

The species may be separated by the following key:—

1. Supplementary groups of disc pores present on the ventral side of the body anterior to the normal groups of perivulvar pores *parinarii* Hall.
Without such supplementary groups of disc pores 2.
- 2(1). Perivulvar pores wanting *pattersoni* Green & Laing.
Perivulvar pores in the normal five groups 3.
- 3(2). Pygidial gland spines replaced by broad plate-like structures that are divided apically into two to four processes; they are arranged singly in the usual positions *caffra* Brain (figs. 1, 31).
Pygidial gland spines of the normal simple type 4.
- 4(3). Dorsal pores very few in number; submedian series, where present, represented by one to three pores *chipingae* Hall.
Dorsal pores well represented in both submarginal and submedian series 5.
- 5(4). Submarginal and submedian groups of dorsal pores on segment 5 arranged in a very regular interrupted single line; pores on segment 6 confined to two or three marginally *baphiae* Hall.
Dorsal pores on segment 5 usually numerous, arranged in a regular series but never in a very regular single line: segment 6 with a submarginal group of usually more than 3 pores 6.
- 6(5). Median lobes always with a deep lateral notch, relatively large and prominent except in one species 7.
Median lobes with never more than a faint indication of a lateral notch, usually relatively small 9.

- 7(6). Median lobes squat; gland spines of the pygidial fringe often arranged in groups of three *communis* Hall.
 Median lobes prominent; gland spines arranged in pairs 8.
- 8(7). Gland spines on the pygidium and margins of all but the 1st free abdominal segment long and conspicuous, the longer spines of the pygidial fringe average $50\ \mu$; submedian group of pores on the 6th segment represented by 3 to 5 pores often forming a continuous series with the submarginal group *diospyros* Hall. 377
- Gland spines shorter, particularly marginally of the 2nd and 3rd abdominal segments, the longer spines of the pygidial fringe average $30\ \mu$; submedian group of pores on the 6th segment, if present, represented by a single pore *chionaspiformis* Newstead.
- 9(6). Perivulvar pores numerous; median 2-8, anterior laterals 23-35, posterior laterals 42-65 *fici* Newstead.
 Perivulvar pores less numerous, the corresponding groups containing about half the number of pores 10.
- 10(9). Dorsal pores numerous and on segments 4 and 5 confined to well-defined series; pygidial gland spines small and inconspicuous, the longer spines averaging $10\ \mu$ *scutiae* Brain (fig. 32).
 Segments 4 and 5 with supplementary series of from two to eight pores in addition to the well-defined series; pygidial gland spines relatively conspicuous, the longer spines averaging $30\ \mu$ *berliniae* Hall.

Genus *Ambigaspis* MacGillivray.

Genotype:—*Pseudaonidia lycii* Brain.

Diagnosis.

Referable to the tribe Diaspidini. Body more or less turbinate in shape, broadest in the thoracic region with anterior margin flatly rounded and lateral margins more or less parallel but with the mesothorax on either side tending to be produced. Thoracic region strongly sclerotised. Lateral margins of prepygidial segments clearly produced. Pygidium broadly rounded with three pairs of lobes. Median lobes neither zygotic nor yoked together and with only a pair of setae between their bases. All lobes with their axes somewhat convergent, acutely rounded apically with well-developed small scleroses arising from the inner and outer angles of the bases of each. Second and third lobes not duplex. Gland spines occurring in the usual positions in twos or threes, except between the median and second lobes, where there is apparently only one. Dorsal and marginal pores relatively small with no very definite arrangement on the pygidium but on the prepygidial segments submedian groups are distinct and well separated from those of the margin and submarginal areas. Gland tubercles present in the usual positions. Perivulvar pores wanting. Anal orifice near the base of the pygidium.

Scale of the adult female more or less circular, low convex, dull brown with exuviae well within the margin. Male scale greyish-white uncarinated with terminal exuvia.

Notes.

This genus at present contains the type species only. It was originally described as a *Pseudaonidia*, and MacGillivray in erecting a new genus for its reception also assigned it to the Aspidiotini. Ferris (1938a: 58) pointed out that the species is definitely Diaspidine, and this is undoubtedly the case, despite certain unusual features. It is a peculiar form of uncertain affinities.

Lindinger (1937: 178) placed this genus as a synonym of *Epidiaspis* Cockerell, a genus from which, in the author's opinion, it is quite distinct.

Genus *Andaspis* MacGillivray.

The genotype—*hawaiiensis* Maskell—which is known from the tropical and subtropical regions of various parts of the world occurs in Africa. *Lepidosaphes punicae* Laing is also assigned to this genus, despite obvious differences from the genotype. It may have to be removed at a later date, but for the time being it is best included here. The two species may be separated as follows:—

1. Each median lobe with a conspicuous club-shaped sclerosis extending inwards from the basal median angle; absence of dorsal ducts posterior to the 4th segment; a sclerotic spur at the anterior lateral angle of both segments 3 and 4 *hawaiiensis* Maskell.
- Each median lobe with a small outer and inner sclerotic incassation; a relatively large irregularly elongate group of dorsal pores on the pygidium of the same size as those of the regular series on segment 4 and much smaller than the large and conspicuous marginal pores; anterior lateral angles of segments 3 and 4 without sclerotic spurs *punicae* Laing.

Brain recorded (1919: 220) *Howardia moorsi* Doane & Ferris from S. Africa. This name has since been sunk as a synonym of *A. hawaiiensis* Maskell.

Genus *Aonidomytilus* Leonardi.

Three species are included in this genus, *A. albus* (Cockerell), of which *Coccomytilus dispar* Vayssière is a synonym, *Lepidosaphes brachystegiae* Hall and *L. mazoensis* Hall, the two latter from S. Rhodesia. According to Ferris (1937: 5) this genus is strictly New World; *albus* Cockerell has probably been introduced into Africa, but it is doubtful if the same is true of the other two species. *A. brachystegiae* differs from the genotype in the presence, in some specimens, of a small tuberculiform process at the anterior lateral angle of abdominal segments 2 and 3, but the development of these varies considerably; in some individuals they are clear, whilst in others they are doubtfully present; *mazoensis* differs in having a marginal macropore between the bases of the median lobes. Apart from these differences, the two species bear a close resemblance to *Aonidomytilus*, and they may well be placed here, at least until the African fauna is better known.

The three species may be separated as follows:—

1. With a marginal macropore between the median lobes; median lobes separated by a distance nearly the width of one; perivulvar pores present *mazoensis* Hall.
- Without a marginal macropore between the median lobes; median lobes set close together; perivulvar pores present; if median lobes separated by a distance nearly the width of one, perivulvar pores are wanting 2.
2. Median lobes set apart by about the width of one; gland spines of the pygidial margin simple and sharply pointed; perivulvar pores wanting *albus* Cockerell.
- Median lobes set close together; gland spines of the pygidial margin, particularly those towards the base, forked at the apex; perivulvar pores in five groups *brachystegiae* Hall.

Genus *Asymmetraspis* MacGillivray.

Genotype:—*Chionaspis distorta* Newstead (fig. 33).

Diagnosis.

Referable to the tribe Diaspidini. Body oval with the anterior half strongly sclerotised and sometimes distorted. Median lobes with their bases yoked together but not zygotic;

with a pair of setae between the lobes but no marginal macropore. Second lobes, if present, poorly developed. Marginal gland spines very small and inconspicuous. Marginal pores relatively small and rather inconspicuous. Dorsal pores similar in size to the marginal pores, few in number but arranged in definite rows on the 4th, 5th and 6th segments. Anal and genital orifices situated near the base of the pygidium. Perivulvar pores wanting.

Scale of adult female small, white, narrow and strongly convex.

Notes.

This genus contains only the type species described from S. Africa on *Protea hirta*. It is very close to *Bantudiaspis* Hall, from which it differs in lacking a marginal pore between the bases of the median lobes, in having the dorsal pores, few though they may be, in well-defined series and in having the anal and genital apertures situated near the base of the pygidium. It is quite possible that further species may be found bridging the present gap between the two genera, and it may be regarded of some significance that *A. distorta* (Newstead) and *B. faureae* (Hall) should both occur on plants belonging to the PROTEACEAE, but for the present the two genera are regarded as distinct.

Brain (1920 : 102) placed *distorta* Newstead as a synonym of *Chionaspis* (*Dinaspis*) *distincta* Leonardi. Examination of type material of the former and material of the latter determined by Brain himself show the two species to be entirely different. MacGillivray included *Chionaspis tenuidisculus* Newstead and *C. dura* Newstead in the genus but in the author's opinion these species are definitely not congeneric with *distorta* Newstead.

Genus *Augulaspis* MacGillivray.

Genotype :—*Chionaspis nudata* Newstead (figs. 2, 34).

Diagnosis.

Referable to the tribe Diaspidini. Body broadly fusiform with groups of small parastigmatic pores associated with both anterior and posterior spiracles. Pygidium broadly rounded with two pairs of lobes. Median lobes well separated by a deep notch, but with their bases not yoked together and without gland spines or marginal pores between; second lobes small and duplex. Gland spines of the pygidial fringe apparently confined to a single spine in each of the first two interlobular spaces. Dorsal pores with short ducts very numerous and arranged in regular broad bands; on the 6th segment the submarginal and submedian series are confluent and consist of about 50 pores; on the 7th segment only the submarginal series is present; on segments 5 to 3 the series are separated but anterior to this, as far as the mesothorax, the pores become fewer and the series are not clearly separated. Gland tubercles doubtfully present but, if present, very small and inconspicuous. Perivulvar pores present. Anal orifice situated towards the base of the pygidium.

Scale of adult female opaque white, convex, broadened posteriorly, rather thick and coarsely striated transversely with golden exuviae. Male scale white, flat and uncarinated.

Notes.

This genus is so far represented only by the type species from Tanganyika. It bears a strong resemblance to *Versiculaspis* MacGillivray, from which it differs in having large groups of perivulvar pores, and in lacking the conspicuous inwardly directed (but not fused) sclerotic bands arising from the bases of the median lobes and the group of conspicuous gland tubercles on the 5th segment.

Genus *Aulacaspis* Cockerell.

This genus is not of African origin and probably all the six species here included have been introduced. Whether *tegalsensis* Zehntner and *madiunensis* Zehntner, both originally described from Java on sugar-cane, are correctly assigned may be open to question; the median lobes have not the appearance of being sunken into the apex of the pygidium although they have a small notch separating them. Another Oriental species having similar characters is *A. wakayamaensis* Kuwana, described from Japan (1926 : 33). *A. herbae* Green has hitherto been placed in the genus *Chionaspis*, but in the author's opinion it would be more properly placed in *Aulacaspis*. *A. cinnamomi* var. *mangiferae* Newstead is here regarded as a synonym of *A. cinnamomi* Newstead.

The species may be separated as follows :—

1. Median pygidial lobes prominent and not appearing sunken in an apical indentation of the pygidium; not divergent 2.
Median lobes not prominent, sunken and divergent 3.
- 2(1). With four pairs of pygidial lobes, the lobules of the three lateral pairs being well developed and of more or less uniform size; prothorax with a well-developed lateral process on either side. *madiunensis* Zehntner.
With three pairs of lobes, the outer lobules of the 2nd and 3rd pairs smaller than the inner lobules; thoracic margin broadly and evenly rounded *tegalsensis* Zehntner.
- 3(1). Margin with well-developed thoracic processes 4.
Margin without thoracic processes 5.
- 4(3). Body relatively large; perivulvar pores numerous, median 31, anterior laterals 55, posterior laterals 19; with about 7 gland spines marginally of segment 4 on each side *fulleri* Cockerell (figs. 3, 35).
Body relatively small; perivulvar pores much less numerous, about half those quoted for *fulleri*; with usually only 2 gland spines marginally of segment 4 *cinnamomi* Newstead.
- 5(3). Female scale circular; 2nd and 3rd lobes prominent, with the lobules longer than broad; with usually 3 gland spines laterally of the 4th segment on either side *rosae* Bouché.
Female scale of irregular shape, usually broadly pyriform; 2nd and 3rd lobes squat with the lobules broader than long; with usually more than 3 gland spines laterally of the 4th segment. Associated with Gramineae *herbae* Green.

Genus *Balaspis* gen. n.

Genotype :—*Balaspis faurei* sp. n.

Diagnosis.

Referable to the tribe Diaspidini. Body oval in outline when mounted, at most very faintly sclerotised with the exception of the pygidium and with margins of free abdominal segments not strongly produced laterally. Pygidium broadly rounded with three pairs of small obconical lobes, median lobes neither zygotic nor yoked together basally, without a macropore but with a pair of gland spines between them; second and third lobes duplex. Gland spines of the pygidial fringe in groups of from 2 to 4 spines. Dorsal pores in well-defined interrupted series on the 3rd, 4th and 5th segments, on the 6th segment the series is continuous. Similar pores occur marginally of all segments as far anterior as the anterior spiracles. Gland tubercles extremely few and inconspicuous. Just posterior to both the anterior and posterior spiracles are loose groups of minute tubular pores. Perivulvar pores wanting. Anal orifice situated towards the base of the pygidium.

Scale of adult female white, moderately to highly convex, rather strongly broadened posteriorly, exuviae of an amber shade. Male scale white, parallel sided, uncarinated.

Notes.

This genus is erected for the reception of a single species from S. Africa, described below. It comes close to *Mitulaspis* MacGillivray, from which it differs in body shape, in lacking the characteristic nature of the lateral margins of the free abdominal segments, the absence of a macropore between the median lobes and the definite arrangement of the dorsal pores of the pygidium into series.

Balaspis faurei sp. n. (figs. 4, 36).

Scale of adult female small white, moderately to highly convex according to position; in the former case rather strongly broadened posteriorly; in the latter not so widely broadened. Exuviae amber coloured. Secretionary appendix with faint irregular transverse striations. Ventral scale persistent along the lateral margins.

Male scale white, with parallel sides, uncarinated.

Length of scale of adult female 1.25–1.5 mm.; breadth 0.8–1.0 mm.

Body of adult female more or less oval in outline when mounted, and at most very faintly sclerotised except for the pygidial region. Antennal tubercle with two or three minute processes and usually two setae of more or less equal lengths. A group of about 12 parastigmatic glands associated with the anterior spiracles. Margins of abdominal segments not strongly produced laterally. Pygidium with a rather well-defined sclerotic pattern, rounded, with three pairs of small conical lobes, median pair separated by a distance rather less than the width of one, not yoked together at their bases but with a pair of small gland spines between them; second lobes duplex, with the lobules of the same shape as the median lobes, the inner lobules being very little smaller than the median lobes but larger than the outer lobules. Third pair of lobes similar but rather smaller and inconspicuous. Gland spines simple, arranged in the usual positions in groups of two to five spines. Marginal and dorsal pores of uniform size, the latter occurring as far as the 6th segment, on which there is a well-defined series running from the submedian area to the margin; on segments 5, 4 and 3 the pores are arranged in well-defined series interrupted to form submedian and submarginal series. Groups of similar pores occur marginally of all segments as far as the anterior spiracles. Submedian series do not occur anterior of the 3rd segment but are replaced by a few scattered pores of a much smaller size; groups of these pores occur just posterior of the posterior and anterior spiracles. Gland tubercles extremely few and inconspicuous, never more than one or two present. Perivulvar pores wanting. Anal orifice situated towards the base of the pygidium.

On *Euphorbia* sp., Sutherland District, Cape Province, coll. J. C. Faure, Nov. 1917, S.N. 2487; Robertson, Cape Province, coll. Van der Merwe, Jan. 1920, S.N. 2484. In both cases the material consisted of pieces of heavily infested small branches.

This species is named in honour of an eminent entomologist—Professor J. C. Faure of the Transvaal University, Pretoria.

Genus *Bantudiaspis* Hall.

This genus, as has already been indicated (p. 504), is extremely close to *Asymmetraspis* MacGillivray. At present these two genera are known only from S. Rhodesia and S. Africa. The species show a decided preference for crevices in the bark and, being small, would be very inconspicuous were it not for the fact that the scales are often white. It is probable that other species will be found in due course.

In addition to the type species—*loranthi* Hall—*faureae* Hall is included. Both species are from S. Rhodesia. A third species, *rhusae* Hall, is here united with *loranthi* Hall, a name which has page preference. A study of the series of slides of the two species now available shows that there are not sufficient constant differences to permit separation. On the other hand, there are differences in the shape and texture of the female scales. They are always small, but in the material from the different host plants examined may vary from very low convex, when they are subcircular or very broadly pyriform, to highly convex when they are narrowed and little broadened posteriorly. On *Rhus* the scales are pale brown and although not particularly thin have a semitranslucent appearance; on *Loranthus* they are more nearly white, whilst on *Turraea nilotica* (MELIACEAE) they are definitely white. Specimens on *Rhus legali* from Cape Province were identical with those of typical *rhusae* from S. Rhodesia. The form on *Loranthus* is intermediate between those on *Rhus* and *Turraea* with no sharp dividing line between those on *Rhus* and *Loranthus* on the one hand and *Loranthus* and *Turraea* on the other. In view of this, all the material is united under the name *loranthi*.

Ferris (1937 : 123) drew attention to the similarity between *Bantudiaspis loranthi* (Hall) and his *Situlaspis multipora*, which he referred with some doubt to *Situlaspis*. The same author later (1941 : 274) erected a new genus *Crassaspis* with *multipora* as type. In so doing, he remarked that in the light of further study the resemblance between the two species above mentioned had become much reduced, and he remarked that the genera *Crassaspis* and *Situlaspis* were apparently of the same stock as *Diaspis* and *Epidiaspis* Cockerell, and that this stock, while highly developed in the Neotropical region, is also represented in eastern Africa. The genera *Asymmetraspis* MacGillivray and *Bantudiaspis* represent African offshoots from this stock.

B. loranthi Hall and *B. faureae* Hall may be separated as follows :—

1. Dorsal pygidial pores definitely smaller than the marginal pores; second pygidial lobes either wanting or extremely inconspicuous . . . *faureae* Hall.
- Dorsal and marginal pores of much the same size; second lobes duplex, small but clearly represented; third lobes very poorly developed . . . *loranthi* Hall.

Genus *Carulaspis* MacGillivray.

Brain (1924 : 14) recorded *Diaspis carueli* Targioni on *Cupressus* from S. Africa, and later Munro and Fouché (1936 : 86) recorded it on *Cupressus*, *Juniperus*, *Thuja* and *Viscum* from the same country. Specimens of this species from the Ethiopian region have not actually been seen by the author, but there is no reason why it should not have been introduced into S. Africa.

MacGillivray erected a genus *Carulaspis* with *Aspidiotus juniperi* Bouché as type, but this species, as well as *Diaspis carueli* Targioni, are now recognised as synonyms of the earlier *Coccus visci* Schrank, which latter species therefore becomes the type of the genus. The separation of *Carulaspis* from *Diaspis* Costa is based on the presence of a small pair of gland spines between the median lobes and the reduction of the pores on segment 6 to a single submarginal pore in the former genus.

Genus *Chionaspis* Signoret.

It was customary for the earlier authors to place in the genus *Chionaspis* all those species in which the female scales were white and elongate, broadened posteriorly to a greater or lesser degree, with terminal exuviae. Later authors placed some of the species of this general type in other genera, but of the

200 odd known species of the tribe Diaspidini from the Ethiopian region over one-third have been placed either directly or indirectly in the genus *Chionaspis*. This is some indication of the strong development of the species of this same superficial appearance.

Chionaspis salicis L., the type of the genus, has the following characters:—

The dermis of the adult female, with the exception of the pygidium, not sclerotised. Median pygidial lobes projecting from the margin with their inner angles extremely close together and with a conspicuous basal sclerotic yoke, but without pores or gland spines between them. Second lobes present and clearly duplex, smaller than the median lobes. Gland spines well developed and in pairs. Dorsal pores in well-defined segmentally arranged rows which are interrupted to form submedian and submarginal series; the submedian series extend as far as segment 6 but the submarginal series do not occur beyond segment 5. The pores of the submedian series on segments 3 and 4 are definitely smaller than those of the corresponding series on segments 5 and 6. Perivulvar pores present.

Of all the *Chionaspis* species from the Ethiopian region that have been seen, only two are retained here—*sterculiae* Laing and *lutea* Newstead. *Chionaspis sterculiae* has some claims to be retained in the genus but it differs from the genotype of *Chionaspis* in being narrowly elongate with faintly but clearly sclerotised dermis, the absence of a submedian series of pores on segment 6 and the median area of the thoracic and 1st and 2nd abdominal segments with numerous tubercles. It is only retained in the genus with considerable hesitation, but it is thought best to adopt this course until the Ethiopian fauna is better known.

Chionaspis lutea Newstead has no claims whatever to inclusion in the genus, but in view of the problem it presents it has been left there for the time being. The species was originally described as a *Chionaspis* by Newstead (1911a: 169) from Amani, Tanganyika, on a forest tree. The same author later (1917a: 133) recorded it as *Chionaspis* (*Phenacaspis*) *lutea* from the Gold Coast on *Funtumia* (APOCYNACEAE) with the statement "the male puparia associated with the females in this colony are very strongly tricarinate and not at all like those in the type lot described from East Africa. Possibly the West African examples belong to a species of *Diaspis*. The ♀♀ are specifically identical with the co-types of *C. lutea*."

A very small piece of the original material from Amani, carrying some female but no male scales, has been available for examination. Figs. 5, 6 and 37 have been drawn from these specimens. It will be seen at once that it is not a *Chionaspis*. Further, the median lobes are clearly not yoked together basally, they have a marginal macropore between them and the nature and arrangement of the dorsal pores on the pygidium are characteristics which preclude its inclusion in *Phenacaspis*. The characters of the pygidium (fig. 37) are typical of *Diaspis*, yet the body shape (fig. 5) is not turbinate as found in that genus and the female scale is typically Chionaspiform with terminal exuviae (fig. 6). The shape of the scales shows considerable variation according to position, some being narrowly elongate whilst others are much broadened posteriorly. The specimen figured represents an intermediate form, but in every case the exuviae are definitely terminal. Were it not for this, one would have no hesitation in assigning it to the genus *Diaspis*.

Genus *Coccomytilus* Leonardi.

Four species have at one time or another been referred to this genus—*dispar* Vayssière, which is now accepted as a synonym of *Aonidomytilus albus*

Cockerell, *bambusicola* Cockerell, which is here referred to the genus *Kuwanaspis* MacGillivray, *chitinosus* Lindinger and *somalensis* Malenotti. The last two species have not been seen, but from the descriptions it would appear to be quite clear that neither is congeneric with *convexa* Maskell, the type species of *Coccomytilus*.

Genus *Contigaspis* MacGillivray.

Genotype:—*Chionaspis subnudata* Newstead (figs. 8, 40).

Diagnosis.

Referable to the tribe Diaspidini. Body fusiform or broadly fusiform with membranous dermis. Pygidium broadly rounded with a pair of small and inconspicuous median lobes which are not only zygotic but, over their basal halves at least, in the closest apposition. Other lobes wanting. Marginal gland spines small and inconspicuous. Marginal and dorsal pores of much the same size, the latter not arranged in well-defined series. Submedian groups on the 5th and 6th segments represented by a few pores, which are replaced typically on the segments anterior to these by pores of a very much smaller size. Scattered pores occur in the marginal areas from the pygidium to the anterior spiracles and a few gland tubercles are present in the usual positions. Perivulvar pores present. Anal orifice situated slightly towards the base of the pygidium.

Scale of adult female, small, white, low convex and broadened posteriorly. Male scale tricarinate or at least with a median carina.

Notes.

This genus comes close to *Africaspis* MacGillivray and *Gadaspis* Hall; from the former it differs in lacking the characteristic sclerotisation associated with the marginal pores of the first two interlobular spaces, in the smaller size of the median lobes and the poor development of the pygidial gland spines; from the latter it differs in having relatively small and not prominent lobes that are not in the closest apposition throughout the entire length of their inner margins, and in the poor development of the pygidial gland spines.

Indigoferae Hall, *cyanogena* Cockerell and a new species described below are included in addition to the genotype. MacGillivray himself included only the genotype and *scutiae* Brain, but the latter species is referable to *Africaspis* MacGillivray. It may also be pointed out that MacGillivray gave as a major character for separating the genus in his key "pygidium of adult female always without plates." In both *subnudata* and *scutiae* plates—or gland spines as they are referred to in this paper—are definitely present, small and inconspicuous though they may be.

When describing *subnudata*, Newstead drew attention to the fact that it was closely allied to *nudata* Newstead. It is not clear on what grounds this statement was made, as an examination of part of the type material of both species shows them to be very different.

Contigaspis naudei sp. n. (figs. 7, 39).

Scale of adult female small, white, with a smooth rather glossy surface that is often partially obscured by extraneous matter, moderately to highly convex and moderately broadened posteriorly. Exuviae very pale lemon coloured. Ventral scale very thin, remaining adherent to the host plant.

Male scale very small with more or less parallel sides and apparently with a median carina only.

Length of scale of adult female 1.0-1.2 mm.; the width and convexity vary considerably according to position.

Body of adult female broadly oval in outline when mounted, membranous except for the pygidial region. Antennal tubercles with a single curved seta. A group of 10-15 parastigmatic glands associated with each anterior spiracle and one of about 4 with each posterior spiracle. Pygidium with only the median pair of lobes represented; these are zygotic with a truncheon-shaped sclerosis arising from the point of zygotis: each lobe has a single deep notch in the outer lateral margin. Gland spines simple, occurring in pairs in the usual positions. Dorsal pores not arranged in well-defined series, submedian groups confined to the 3rd to the 6th segments, the number of pores in each group usually 3 or 4. Similar pores occur in the marginal and submarginal regions of all segments as far anterior as the mesothorax. Gland tubercles rather numerous, occurring in the usual positions, as far as the vicinity of the anterior spiracles. Perivulvar pores in five groups, median 5-10, anterior laterals 11-20, posterior laterals 11-16 (average of 18 examples 8:14:15). Anal orifice situated near the centre of the pygidium.

On small twigs of *Cassia mimosoides* (LEGUMINOSAE), ZULULAND: Port Durnford, coll. P. C. Kotze, 20.xii.26.

I have pleasure in naming this species after Dr. T. J. Naudé, Chief of the Division of Entomology, Pretoria, through whose kindness I have been able to examine many of Brain's species that would not otherwise have been available to me.

The four species here included in the genus *Contigaspis* MacGillivray may be separated as follows:—

1. Median lobes falling away laterally with one or two deep and conspicuous notches; dorsal pores of the submedian groups on segments 3 to 6 of uniform size 2.
- Median lobes more or less quadrate, usually with no trace of a lateral notch or at most with only a faint indication of a notch; pores of the submedian groups on segments anterior to the 5th replaced by others of a much smaller size 3.
- 2(1). Median lobes with a single deep lateral notch; small but prominent and about as long as broad. *naudei* sp. n. (figs. 7, 39).
Median lobes with two lateral notches, small, not prominent and distinctly broader than long *cyanogena* Cockerell (fig. 38).
- 3(1). Median lobes relatively large and prominent (each lobe about 12 μ broad); setae of the 1st interlobular spaces short, not extending beyond the apices of the median lobes *indigoferae* Hall.
Median lobes small and inconspicuous (each lobe about 8 μ broad); setae of the 1st interlobular spaces long, three or four times the length of the median lobes *subnudata* Newstead (figs. 8, 40).

Genus *Cooleyaspis* MacGillivray.

Genotype :—*Chionaspis praelonga* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body very narrow and elongate with roughly parallel sides. Pygidium rounded. Median lobes with their bases yoked together, but separated by a rather deep U-shaped notch. Second lobes duplex, well developed, the inner lobules being just as large and usually larger than the median lobes. Dorsal pores in well-defined regular interrupted series, the submedian series extending as far as the 6th segment, but the submarginal series not occurring beyond the 5th segment. Marginal macropores and gland spines in the usual positions, the latter arranged singly. Perivulvar pores in five groups

which tend to be confluent; on the segment preceding a supplementary transversely orientated group of similar pores. Anal orifice near the base of the pygidium. Margin of prepygidial segments as far as the metathorax, with numerous pores similar to the dorsal pores on the pygidium and a few gland tubercles in the usual positions.

Scale of adult female white, very elongate and narrow, with parallel sides and complete ventral scale. Male scale white and very faintly tricarinate.

Notes.

This genus belongs to the *Phenacaspis* Cooley & Cockerell, *Rolaspis*, *Tecaspis*, *Voraspis* group of genera, from all of which it is differentiated by the curious transverse group of supplementary pores. The number and arrangement of these pores is unlike that found in the species which have in the past been assigned to *Poliaspis*. Only the type species is known at present.

Genus *Coronaspis* MacGillivray.

MacGillivray assigned *Chionaspis auratilis* Newstead from Uganda to this genus, the type of which is a Ceylon species—*C. coronifera* Green. In the author's opinion *auratilis* is not congeneric with *coronifera*, the male scales are quite different, and in *auratilis* the second lobes are strikingly larger than the median lobes and the pygidial fringe different.

Genus *Credodiaspis* MacGillivray.

This genus was erected by MacGillivray for a single species—*Cryptodiaspis limuloides* Lindinger—from the Cameroons. In the key to genera given by that author the only character separating it from the genus *Cryptodiaspis* Lindinger is the absence of perivulvar pores. This in itself would be insufficient grounds for the separation but unfortunately neither *limuloides* nor the other two species of *Cryptodiaspis* have been seen and no opinion can, therefore, be expressed.

Genus *Cryptodiaspis* Lindinger.

This genus was erected by Lindinger for three species from the Cameroons. As stated above, these species have not been seen, but judged from the descriptions the genus is valid and the three species assigned to it form a well-defined little group.

Genus *Daraspis* gen. n.

Genotype:—*Chionaspis bussii* Newstead (figs. 9, 41).

Diagnosis.

Referable to the tribe Diaspidini. Body very long and narrow and all but the pygidium membranous. Pygidium rounded with three pairs of lobes. Median lobes divergent, neither zygotic nor yoked together, but with a notch between, with two gland spines and a marginal macropore between the lobes; second lobes duplex, extending slightly beyond the median pair; third lobes duplex, small and inconspicuous. A pore-carrying process occurs in each interlobular space (except between the median lobes) and there are two more between the 3rd lobes and the base of the pygidium on either side. Five to seven large marginal pores occur on either side of the median lobes. Gland spines occurring singly in the usual positions except at the base of the pygidium, where there is a pair. Dorsal pores very much smaller than the marginal pores, very few in number and apparently without any regular arrangement. Dorsal pores on the prepygidial segments of a similar small size and few in number and not found anterior of the posterior spiracles. Gland tubercles wanting except marginally

of the 3rd segment, where there are two unusually large tubercles, each of which carries, usually, 3 microducts. Perivulvar pores present. Anal orifice situated near the base of the pygidium.

Scale of adult female, flat, narrowly elongate with broadly flattened margin not much broadened posteriorly, translucent pale brown with golden exuviae. Male scale brown, more or less parallel-sided and uncarinated.

Notes.

This genus at present contains only the type species from French Guinea. It comes closest to *Sinistraspis* MacGillivray, from which it differs in the median lobes not being yoked together, in having a marginal macropore and two gland spines between the median lobes and in lacking any asymmetrically developed characteristic.

Genus *Dentachionaspis* MacGillivray.

Genotype :—*Chionaspis capensis* Newstead, which is regarded as a synonym of *Dinaspis lounsburyi* Leonardi.

Diagnosis.

Referable to the tribe Diaspidini. Body fusiform with the anterior half moderately sclerotised at maturity. Pygidium broadly rounded with two pairs of lobes. Median lobes small, widely separated by a marginal notch, with scleroses arising from their bases, which are usually incompletely fused and not forming a completed yoke. Second lobes duplex with inner lobules typically much larger than the outer lobules and larger than the median lobes. Without gland spines or marginal pore between the median lobes. Gland spines of the pygidial fringe arranged singly; these are forked at the apex in the genotype but simple in the other included species. Marginal pores in the usual positions. Dorsal pores arranged in definite segmental series as far as the 5th segment; on the 6th segment the submedian group is represented by 3 to 6 pores but the submarginal group is reduced to 2 or 3 marginally. Prepygidial and metathoracic segments with groups of pores marginally and groups of gland tubercles in the normal positions. Perivulvar pores wanting in the type species. Anal orifice situated towards the base of the pygidium.

Scale of the adult female highly convex, white and moderately broadened posteriorly. Male scale small, white, uncarinated.

Notes.

This genus comes closest to *Inchoaspis* MacGillivray, but the species of the latter genus are very much larger—unusually large—in addition to other differences of a less striking nature.

Dinaspis pittospori Hall from S. Rhodesia, *Chionaspis margaritae* Brain from S. Africa, *Chionaspis pseudonivea* Malenotti from the Italian Somaliland, *Chionaspis auratilis* Newstead from Uganda and *Chionaspis ritchiei* Laing from Tanganyika and Sierra Leone are included in addition to the genotype.

Dinaspis pittospori differs from the genotype in the much shallower nature of the notch between the median lobes, whilst *margaritae* differs in having five well-developed groups of perivulvar pores, but despite this it appears to be more nearly congeneric with *lounsburyi* Leonardi than *pittospori*. Brain remarks (1919 : 231) that *margaritae* is very much like *Chionaspis capparis* Brain, a species which later (: 234) he refers to as being similar to *Dinaspis lounsburyi* Leonardi in some respects. *Chionaspis capparis* has not been seen, but it seems probable that it also should be included in this genus.

Chionaspis pseudonivea, like *pittospori*, has a shallow notch between the

median lobes and bears a close resemblance to it, but like *margaritae* it has five groups of perivulvar pores.

Chionaspis auratilis and *ritchiei* differ from the genotype and other species in having a much narrower body shape, and, although both possess certain other marked differences, they bear a sufficiently close resemblance to the genotype to be placed here until the fauna is better known. In *auratilis* the antennal tubercles are set unusually close together and immediately anterior to the rostrum, and the male scale is dull gold in colour. In *ritchiei* it is not certain that the so-called long setae of the pygidial fringe are really setae; the writer suspects that they are slender gland spines, but the capitate heads are admittedly obscure. It may be noted that most examples of this species seen exhibit a few supplementary disc pores anterior to the groups of perivulvar pores.

Dinaspis berlesei Malenotti, from the Italian Somaliland, also certainly belongs to the genus *Dentachionaspis* and is very probably the same as *lounsburyi* Leonardi, but the only preparation seen—ex coll. Malenotti and bearing the data of the type material—is not sufficiently good to enable a definite opinion to be expressed.

The six included species may be separated as follows :—

1. Perivulvar pores present 2.
- Perivulvar pores lacking 4.
- 2(1). Body of adult female long and narrow; pygidial gland spines replaced by long setae(?) which are more slender than is usual for gland spines but stout for setae *ritchiei* Laing.
- Body of adult female fusiform; gland spines well developed and of normal form 3.
- 3(2). With a deep notch between the median pygidial lobes; on the ventral aspect of both abdominal segments 4 and 5 four or five small gland tubercles, usually one pair in a submarginal and another pair in a submedian position; perivulvar pores relatively numerous, averaging, median 8, anterior laterals 21, posterior laterals 37 *margaritae* Brain (figs. 10, 42).
- With a shallow notch between the median lobes; gland tubercles on segments 4 and 5 lacking; perivulvar pores fewer, averaging, median 8, anterior laterals 8, posterior laterals 14 *pseudonivea* Malenotti (figs. 11, 43).
- 4(1). Body of adult female long and narrow; antennal tubercles set unusually close together and immediately anterior to the rostrum; male scale dull gold in colour *auratilis* Newstead.
- Body of adult female fusiform; antennal tubercles not set unusually close together and normally placed; male scale white 5.
- 5(4). Median lobes acutely pointed, separated by a relatively deep notch; gland spines of the pygidial fringe often with forked tips *lounsburyi* Leonardi.
- Median lobes rounded, separated by a very shallow notch; gland spines simple *pittospori* Hall.

Genus *Dentaspis* MacGillivray.

Genotype :—*Chionaspis substriata* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body small, fusiform to globose with delicate hyaline dermis. Mouthparts, typically, unusually close to the anterior margin. Anterior spiracles situated in a shallow but clearly defined pit. Pygidium broadly to very broadly rounded

with two pairs of lobes. Median lobes widely separated and small; in the type and two other species they are squat, broader than long with serrated apices; in two other species they are narrowly conical; second lobes in the former case duplex, of the same shape as the median pair; in the latter case single, larger than the median lobes and rounded apically. Median lobes not yoked together and without gland spines or marginal pore between them (in the type species a marginal pore is sometimes present). Gland spines of the pygidial fringe occurring singly. Dorsal pygidial pores relatively large, with short ducts either scattered or at least without any definite arrangement into series or rows. Similar pores occur marginally as far anterior as the anterior spiracles but are not numerous; gland tubercles relatively few. Perivulvar pores may or may not be present. Anal orifice situated slightly anterior of the middle of the pygidium.

Scale of adult female very highly convex, white or silvery white, often with transverse striations, rather narrow. Male scale white with or without a median carina.

Notes.

This genus is probably African and comes closest to *Inchoaspis* MacGillivray, but in that genus the females are unusually large, whereas in *Dentaspis* the reverse is the case.

In addition to the type four other species are included here. They are all small species in which the female scale is very highly convex and the adult female usually globose, with such delicate hyaline dermis that it is difficult to secure preparations showing the pygidial margin satisfactorily. The mouth-parts are set unusually close to the anterior margin, and this is particularly true in the cases of *substriata* and *rugosa*.

The five species fall into two groups, *substriata*, *globosus* and *rugosa* forming one and *hargreavesi* and *gibber* the other. The *substriata* group is characterised by having squat median lobes broader than long and apically serrated and duplex second lobes of similar shape. The *hargreavesi* group have conical median lobes and simple second lobes that, in the case of *hargreavesi*, are much longer than broad and more prominent than the median pair.

Despite the obvious differences between the two groups there are definite resemblances between *substriata* and *hargreavesi* on the one hand and *globosus* and *gibber* on the other which it is difficult to describe.

The five species may be separated as follows:—

1. Perivulvar pores present; median and second lobes squat, broader than long and apically serrate; second lobes duplex 2.
Perivulvar pores wanting; median lobes conical, second lobes conical or elongate and rounded apically, not duplex 4.
- 2(1). Perivulvar pores restricted to the posterior lateral groups and consisting of one or two pores *substriata* Newstead.
Five small groups of perivulvar pores present 3.
- 3(2). Median lobes separated by a distance equal to about three times the width of one; pygidial gland spines conical in form, much swollen at the base *rugosa* Hall.
Median lobes separated by a distance equal to about the width of one; pygidial gland spines not conspicuously swollen basally *globosus* Brain (figs. 12, 44).
- 4(1). Second lobes consisting of a single prominent lobule much longer than broad and much more prominent than the median lobes, of much the same width throughout and rounded apically *hargreavesi* Laing.
Second lobes consisting of a single lobule little if any more prominent than the median lobes; about as broad as long, tapering, with rounded tip *gibber* Hall.

Genus *Diaspis* Costa.

Synonymy :—*Umbaspis* MacGillivray. Genotype :—*Diaspis regularis* Newstead.

Notes.

Nine species are included in this genus, of which six have been described as new from Africa. For one of these—*regularis* Newstead—MacGillivray erected the genus *Umbaspis* on the grounds that it differed from *Diaspis* in possessing interlobal truncate lobe-like glandular projections except between the median lobes. Glandular projections in these positions are characteristic of the genus *Diaspis*, but it would be difficult to separate the African species satisfactorily on the basis of this character alone on account of the gradation from truncate to rounded exhibited by the various species. Moreover, there are no other constant differences in characters separating those species which have definitely truncated projections from those in which the projections are clearly rounded. For this reason the genus *Umbaspis* is regarded as a synonym of *Diaspis*.

Of the six species described from Africa all were originally assigned to *Diaspis*.

D. spatulata Hall was described as a variety of *D. subregularis* Hall, but it is now raised to specific rank in view of the fact that the flatly rounded obscurely spinose pore-carrying projection towards the base of the pygidium in *subregularis* is replaced by a conspicuous sharply sclerotised spur in *spatulata*. There are other differences that were indicated when the two forms were described.

Diaspis africana, *parva* and *stilosa* all of Lindinger, and *senegalensis* Vayssi re, also certainly belong to this genus, but they are known only from the descriptions.

The nine included species may be separated by the following key :—

1. With a prominent marginal vasiform appendage near the base of the pygidium. Perivulvar pores absent *helveola* Laing.
- Without such an appendage. Perivulvar pores present 2.
- 2(1). Median lobes neither divergent nor sunken into the apex of the pygidium but projecting *echinocacti* Bouch .
- Median lobes divergent, projecting little, if any, beyond the apex of the pygidium, with the inner margins longer than the outer and forming a definite notch 3.
- 3(2). With a sharply pointed conspicuous sclerotised spur marginally of the 4th segment at its posterior extremity on either side 4.
- Sharply pointed conspicuous sclerotised spur either absent or replaced by a projection of a different form 7.
- 4(3). Pygidium with six or more large pores in a submarginal series orientated with their long axes parallel to the median longitudinal axis of the body; associated chiefly with pineapple *bromeliae* Kerner.
- Pygidium with never more than two or three such pores 5.
- 5(4). Lobules of the 2nd and 3rd lobes markedly dilated apically and sharply truncated *spatulata* Hall.
- Lobules of the 2nd and 3rd lobes neither conspicuously dilated nor sharply truncated 6.
- 6(5). Prothorax usually with well-developed lateral lobes; interlobular glandular projections apically rounded *boissduvalii* Signoret.
- Prothoracic lateral lobes wanting; interlobular glandular projections apically truncated *regularis* Newstead.

- 7(3). Marginal pores considerably larger than the dorsal pores except for two large longitudinally orientated submarginal pores, one anterior to both the 2nd and 3rd lobes on each side, which are as large as the marginal pores 8.
 Marginal pores not strikingly larger than the dorsal pores and the two large submarginal longitudinally orientated pores not present *bicolor* Laing.
- 8(7). Median lobes large, much larger than the lobules of the 2nd lobes; submedian group of dorsal pores present on the 5th segment only and represented usually by a single pore *carissae* Hall.
 Median lobes much the same size as the lobules of the 2nd lobes; submedian groups in small groups on segments 2 to 5 both inclusive *subregularis* Hall.

Genus *Dinaspis* Leonardi.

Seventeen species have been assigned to this genus in the past. These were later reduced to 15 by sinking two names as synonyms. It is the view here that not one of these species can be correctly assigned to *Dinaspis*, and all those that have actually been seen are placed elsewhere in this paper. With the exception of *D. silvestri* Leonardi, not one exhibits the striking difference in size between the marginal pores and dorsal pores which is one of the main characteristics of *Dinaspis*. *D. silvestri*, on the other hand, has a large macropore between the median lobes and differs from typical *Dinaspis* in other respects.

The genotype of *Dinaspis* is a South American species and the genus is probably of South American origin.

Genus *Duplachionaspis* MacGillivray.

Three species are included in this genus, but it is with some hesitation that *ugandae* Hall has been assigned. *Chionaspis paolii* Malenotti, described from the Italian Somaliland on *Mariscus*, is certainly a *Duplachionaspis* and probably the same as *D. asparagi* (Laing & Cockerell), but the only slide available—presumably from the type lot of material as it bears identical data—is not sufficiently good to permit of a definite opinion. *Chionaspis natalensis* Maskell, described from Natal, probably also belongs here but has not been seen.

MacGillivray included 21 species in his genus, of which 11 are African, but the majority of these are clearly not congeneric with *graminis* Green, the type of the genus.

The three included species may be separated as follows:—

1. Pygidium acute; median lobes longer than broad and strongly divergent 2.
 Pygidium broadly rounded; median lobes squat, never longer than broad and at most only slightly divergent *ugandae* Hall.
- 2(1). Pygidial gland spines of the interlobular spaces single, rarely in pairs; submedian groups of dorsal pores of uniform size on segments 3 to 6 *stanotophri* Cooley (figs. 13, 45).
 Pygidial gland spines of the interlobular spaces in pairs; submedian groups of dorsal pores on segments 3 and 4 replaced by pores of a much smaller size. *asparagi* Laing & Cockerell.

Genus *Epidiaspis* Cockerell.

The only species of this genus so far recorded from Africa is *E. ficifoliae* Hall. It is somewhat of a surprise to find this genus represented in Africa, as it was thought to be chiefly New World, apart from the type species, which is European.

Brain (1919 : 228) described a new species as *Diaspis* (*Epidiaspis*) *conspicua*, but this species is not even referable to the Diaspidini; it belongs to the Aspidiotine genus *Morganella* Cockerell.

Genus **Finaspis** gen. n.

Genotype :—*Lepidosaphes distincta* Hall.

Diagnosis.

Referable to the tribe Diaspidini. Body relatively small, elongate and narrow with parallel sides. Dermis, with the exception of the pygidium, with little evidence of sclerotisation but closely and finely striated transversely. Pygidium with a well-defined sclerotised pattern, somewhat acute with three pairs of densely sclerotised lobes. Median lobes large, tridentate, broader than long, set close together, with a small dentiform process covering the point of junction of the inner angles on the dorsal aspect. Median lobes and tissues immediately surrounding densely sclerotised. Second lobes smaller than median lobes, conical; third lobes much smaller than second lobes, but of similar shape. All lobes conspicuous on account of sclerotisation. Marginal gland spines arranged singly in the normal positions, the two towards the base of the pygidium often being dilated and bifurcate or divided apically. Marginal pores wanting with the exception of one on the 5th segment. Dorsal pores very few, small, with short ducts, scattered. Margin of free abdominal segments with a few similar pores and a few gland tubercles. Perivulvar pores in five groups. Anal orifice towards the base of the pygidium.

Scale of adult female very elongate and narrow, dull brown, exuviae terminal. Male scale much smaller than that of the female, white or dirty white, with parallel sides, uncarinated.

Notes.

This genus is difficult to place. It appears to have some affinities with *Africaspis* MacGillivray, but differs from that genus in many obvious respects as, for instance, the absence of sclerotised marginal macropores, gland spines arranged singly, and in the lack of arrangement and small size of the dorsal pores.

Lindinger (1932b : 202) assigned *L. distincta* to *Pygalataspis*, a genus erected by Ferris (1921 : 218) for a new species, *P. miscanthi*, from Formosa. This genus probably belongs to the Odonaspidini, and differs from *Finaspis* in having numerous ducts on the pygidium both dorsally and ventrally, broad toothed plates on the pygidial fringe and the absence of a small conical process between the median lobes.

At present the genus is represented by a single species described from S. Rhodesia on *Zizyphus jujuba*.

Genus *Fiorinia* Targioni.

F. fioriniae Targioni is fairly common throughout South Africa on Camellia and Palms (Brain, 1919 : 221), and it has also been recorded by Lindinger (1910 : 45) from Zanzibar on *Celtis mauritiana* and by the same author (1913 : 77) from Tanganyika on Palms.

F. kewensis Newstead has also been recorded from Tanganyika on *Borassus* by Lindinger (1913 : 77), but no African material of this species has been seen. There is reason to believe that this species may be of Australian origin and incorrectly assigned to *Fiorinia*, but until a comprehensive study of the species—particularly Australian—of this and allied genera has been made, it is best left where it is.

Genus *Furchadaspis* MacGillivray.

Represented by the type species only, of which *Diaspis rhusae* Brain (1919 : 225) is considered to be a synonym. *D. rhusae* was described from *S. Africa* on *Rhus* sp. and later was found by the author on *Cussonia spicata* in Southern Rhodesia and transferred to the genus *Furchadaspis* (Hall, 1941 : 230). *Furchadaspis zamiae* has hitherto been regarded as confined to Cycads and to *Zamia* spp. in particular. The author is unable to separate specimens from the type material of *rhusae* and *rhusae* from *Cussonia* in S. Rhodesia from *zamiae*. The principal difference between the two species was said (Hall, loc. cit.) to be that the two gland spines between the median lobes were simple and not bifurcated. Brain figured them as simple, but further examination of specimens from the type material shows that this is not the case; they are bifurcate or fimbriate, but this is not always apparent on account of the position in which they happen to be. Other differences are not sufficiently marked or consistent to warrant separation.

Genus *Gadaspis* gen. n.

Genotype :—*Chionaspis (Pinnaspis) combrei* Hall.

Diagnosis.

Referable to the tribe Diaspidini. Body elongate, fusiform, with membranous dermis. Pygidium rounded with a large and prominent pair of median lobes, rather longer than broad with their inner margins in the closest apposition. Second lobes, if present, duplex, small and dentate. Third lobes wanting. Margin of the pygidium on either side of the median lobes sometimes recessed. Marginal gland spines in the usual positions, well developed and occurring in groups of 2 to 4 spines, rarely singly. Marginal and dorsal pores of the same size. Dorsal pores arranged in rather loose series as far as the 5th segment; on the 6th segment the pores are more or less confined to the submarginal region and tend to be scattered. Similar pores occur marginally on all segments as far anterior as the mesothorax. Gland tubercles present in rather large groups in the usual positions as far as the anterior spiracles. Perivulvar pores present in five groups. Anal orifice towards the base of the pygidium.

Scale of the adult female white, moderately convex, elongate, pyriform in shape with terminal exuviae. Male scale white, parallel sided and normally uncarinated.

Notes.

This genus comes closest to *Pinnaspis* Cockerell and *Contigaspis* MacGillivray. From *Pinnaspis* Cockerell it differs in having large and prominent median lobes, the nature of the 2nd lobes if any, the presence of pores submarginally on segment 6 and the less regular arrangement of the dorsal pores on the segments anterior to this. From *Contigaspis* it differs in having large and prominent median lobes in the closest apposition and well-developed gland spines on the marginal fringe.

In addition to the type species two others are included to give a very well-defined and characteristic little group. They were all described from S. Rhodesia from *Combretum* and *Uapaca*. They may be separated as follows :—

1. Ventral dermis of the thoracic and anterior free abdominal segments with a few scattered tubercles carrying stout blunt processes. No trace of second lobes. Dorsal pores on the free abdominal segments confined to the marginal area *tuberculata* Hall.

- Lacking such tubercles. Second lobes small, duplex and dentate.
Dorsal pores on the free abdominal segments in addition to the marginal groups distributed at irregular intervals right across the segments. . . 2.
2(1). With a broad and deep indentation of the margin on each side of the median lobes; gland spines of the pygidial fringe in groups of three or four *excisa* Hall.
With no such conspicuous indentation; gland spines arranged in pairs *combreti* Hall.

Genus *Genaparlatoria* MacGillivray.

Material of *G. pseudaspidiotus* Lindinger has been received from the Sudan on Mango. This is believed to be the first record of this species occurring in the African continent.

Genus *Gramenaspis* MacGillivray.

This genus was erected for a single species—*Chionaspis africana* Newstead—described from South-West Africa on a "grass like" plant. Unfortunately neither the type nor any slides or material of this species have been traced. Whether the genus will prove to be valid it is impossible to say, but the characters of the type species given by Newstead seem to suggest that it may prove so.

Genus *Greenaspis* MacGillivray.

Genotype :—*Chionaspis elongata* Green.

Diagnosis.

Referable to the tribe Diaspidini. Body membranous with anterior extremity more flattened than rounded, extremely long and very narrow owing to the prolongation of the thoracic segments, abdominal segments short with the second and third laterally produced. Pygidium acute with two pairs of lobes. Median lobes strongly divergent and prominent, of unusual shape, with their inner edges emarginate and bases yoked together but lacking setae, gland spines or marginal pores between them. Second lobes duplex, the lobules separate, narrow with the inner much the longer. Gland spines of the pygidial fringe long and conspicuous, occurring singly in the normal positions except at the base of the pygidium, where there is a pair. Marginal and dorsal pores of the same size, the latter very few in number, in segmentally arranged rows as far as the 5th segment. Prepygidial and meta-thoracic segments with very small groups of pores and gland tubercles in the usual position. Perivulvar pores present. Anal orifice towards the base of the pygidium.

Scale of the adult female white and extremely long and narrow; male scale white, slightly broadened posteriorly.

Notes.

This genus resembles *Albataspis* MacGillivray, which was erected for an Australian species—*Mytilaspis nivea* Maskell—but this species is only known to the author from the original description.

The genus *Greenaspis* was erected for a Ceylon species, *C. elongata* Green, of which the Green collection contains not only the type but slides of material from India and Formosa.

G. elongata Green has been recorded from Italian Somaliland on *Cassine holstii* (CELASTRACEAE) by Malenotti (1915:349). This seems an unlikely host plant for *elongata*, which has previously only been known from Gramineae, chiefly Bamboo. The record is, therefore, only accepted with reserve.

Genus *Gymnaspis* Newstead.

Three species assigned to this genus have been described from Africa. One of these, *G. faureae* Brain, is not considered to be congeneric with the type on account of the fact that the pygidium of the second-stage female lacks the lobes and plates found in the genotype and other species here referred to the genus. The correct generic position of *faureae* is not clear. In the specimens available for examination, the sclerotisation of the second-stage female completely obscures the pygidial characters. There is even some doubt in the author's mind as to whether it is referable to the tribe Diaspidini at all.

Lindinger placed *G. africana* Newstead in *Cryptaspidiotus* Lindinger, a genus very close to, if not identical with, *Aonidia* Targioni. The ducts in both *africana* Newstead and *bilobis* Green & Laing are only imperfectly two-barred and it is open to question whether a second bar is present. In the larvae of the genotype—*aechmeae* Newstead—the ducts are clearly two-barred. It will be necessary to make a study of all stages of these and allied species before any definite conclusions can be reached. In the meantime the two species included may be separated as follows:—

1. Pygidium of adult female with 3 pairs of lobes; interlobular spaces with plates and in addition three plates anterior of the 3rd lobes

africana Newstead.

Pygidium of adult female with no more than a single pair of prominent median lobes; plates very few, small and inconspicuous, two between the median lobes and two or three immediately lateral of them on each side. *bilobis* Green & Laing.

Genus *Howardia* Berlese & Leonardi.

The only species known from Africa is the type species—*biclaris* Comstock. Other African species that have been referred to this genus in the past are now considered to have been incorrectly placed and have been assigned to other genera in the present paper.

Genus *Hulaspis* gen. n.

Genotype:—*Howardia dombeyae* Hall (figs. 14, 46).

Diagnosis.

Referable to the tribe Diaspidini. Body very broadly turbinate in outline and membranous. Pygidium with a strongly marked sclerotic pattern which is sharply divided into two halves by a funnel-shaped furrow arising from the point of junction of the median lobes. A single pair of median lobes only present, the inner margins of these lobes in close apposition, except at the apical extremity, falling away laterally on either side. Each median lobe with a conspicuous sclerosis arising from its base; the two scleroses are outwardly divergent and each consists of a tube-like structure with very much thickened and sclerotised lateral margins. In the angle between the scleroses, i.e. between the median lobes, is a marginal pore. About 8 gland spines between the median lobe and base of the pygidium on either side; these are of uneven sizes, those towards the base being usually simple whilst those nearer the median lobes are large, often plate-like with bifurcated apices. Gland tubercles, relatively slender and not very numerous, occur as far anterior as the 1st segment. Dorsal pores with the submedian groups well separated from the submarginal groups, not numerous and more or less confined to the 2nd to 5th segments, both inclusive; the submarginal group on the 6th segment may be represented by one or two pores. Perivulvar pores lacking. Anal orifice set towards the apex of the pygidium.

Scale of adult female sub-circular, white, with brown more or less central exuviae; nymphal exuvia rather large, occupying about $\frac{2}{3}$ of the puparium. Male scale not known.

Notes.

Only the type species known at present. This genus comes close to *Howardia*, from which it differs in having definitely zygotic median lobes, the different character of the scleroses at the base of the median lobes, and the entirely different nature and arrangement of the gland spines.

Genus *Inchoaspis* MacGillivray.

Genotype:—*Chionaspis amaniensis* Lindinger, which is a synonym of *C. dentilobis* Newstead.

Synonymy:—*Remotaspis* MacGillivray. Genotype:—*Chionaspis dentilobis* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body large, fusiform with membranous dermis. Parastigmatic pores associated with the anterior spiracles relatively numerous. Pygidium large, broadly rounded, with marginal intersegmental indentations. Median lobes small, widely separated, not yoked together and with neither gland spines nor marginal pore between their bases. Second lobes duplex, larger than the median lobes. Third and, in the genotype, fourth lobes present. Gland spines in the usual positions varying from 0-3 per group. Dorsal pores with short ducts as far as the 5th segment in relatively well-defined series and relatively numerous; on the 6th segment they are also relatively numerous but the arrangement tends to be far less regular. Marginal pores in the normal positions and of the same size as the dorsal pores. Marginal regions of the prepygidial segments with numerous pores similar to those on the pygidium; they also occur on the thoracic segments as far as the anterior spiracles but are more widely separated; relatively large groups of gland tubercles in the normal positions. Perivulvar pores not present in the type species but present in two other species, in one of which supplementary groups occur in addition. Anal orifice towards the base of the pygidium.

Scale of the adult female white to silvery white, highly convex and broadened posteriorly when not contorted and compressed by overcrowding. Male scale white with a median carina.

Notes.

Chionaspis dentilobis was described by Newstead (1910:195) and *C. amaniensis* by Lindinger (1910:42). The latter author later (1913:75) sank his *amaniensis* as a synonym of *dentilobis*. MacGillivray in 1921 created two new genera *Remotaspis* with *dentilobis* Newstead as type (:311) and *Inchoaspis* with *amaniensis* Lindinger as type (:310). *Inchoaspis* has page precedence and is therefore adopted.

Inchoaspis comes closest to *Dentaspis* MacGillivray, but the species are much larger. Lindinger (1937:187) placed it as a synonym of *Chionaspis* Signoret, a genus to which it bears little or no resemblance at all.

Despite obvious differences, the three species here included bear such a strong resemblance to each other that it is difficult to believe they are not congeneric. They may be separated from each other as follows:—

1. With 5 groups of perivulvar pores and with supplementary groups of disc pores on the ventral dermis anterior to these; pygidial fringe without gland spines *argentata* Hall.
- Without perivulvar pores or supplementary disc pores; pygidial fringe with gland spines in the normal positions 2.

2. With three and sometimes four pairs of pygidial lobes, median and inner lobules of the 2nd and 3rd pairs rounded with faintly serrated edges; median lobes separated by a distance no more than twice the width of one; with no marginal pores between the median lobes; gland spines anterior of the second lobes in groups of 3; dorsal pores on segment 6 in a relatively well-defined series *dentilobis* Newstead.
- With two pairs of lobes, median and inner lobules of the second lobes may be rounded or pointed; median lobes separated by a distance nearly four times the width of one; with 2 or 3 marginal pores between the median lobes; gland spines of the pygidial fringe occurring singly; dorsal pores on segment 6 scattered *pygaei* Hall.

Genus *Incisaspis* MacGillivray.

This genus was erected for the reception of a single species—*Diaspis pugionifera* Lindinger—described from the Cameroons. This species has not been seen, but from the original description it seems not improbable that it may prove to represent a valid genus.

Genus *Ischnaspis* Douglas.

Four species of this genus have been described or recorded from Africa, but only two of these have been available for examination—*longirostris* Signoret and *macrolobii* Laing—which may be separated as follows:—

1. Perivulvar porès wanting, their place being taken by four transversely ovate thickenings lying in the middle of a ventral plate-like area; basal club-shaped sclerosis at the base of the inner lobule of the second lobes very slightly constricted in the middle *macrolobii* Laing.
- Perivulvar pores present in five small groups and no ovate ventral thickenings; sclerosis at the base of the second lobe deeply constricted in the middle *longirostris* Signoret.

Genus *Kuwanaspis* MacGillivray.

Material of *K. bambusicola* (Cockerell) on Bamboo has been received from Senegal. This species was originally described from Brazil as a *Mytilaspis*, but it has since been recorded from Algiers by Balachowsky (1928: 139) as well as from elsewhere. This author placed it in the genus *Coccomytilus*, but it is here considered to be referable to the genus *Kuwanaspis* as it possesses a membranous forked process between the median lobes and between the median and second lobes of the type found in that genus. Moreover, as in the case of all the known species of *Kuwanaspis*, it is associated with Bamboo.

Genus *Ledaspis* gen. n.

Genotype:—*Chionaspis (Dinaspis) mashonae* Hall.

Diagnosis.

Referable to the tribe Diaspidini. Body fusiform with anterior half usually more or less heavily sclerotised. Pygidium rounded with median lobes not zygotic, separated by a distinct notch but with their bases yoked; they are squat in the type species but may be prominent. Second lobes duplex, small and somewhat inconspicuous. A pair of small setae between the median lobes, but gland spines and pores wanting. Marginal pores in the usual positions; dorsal pores, of a similar size, arranged in well-defined series as far as the 5th segment; on the 6th segment they show less regular arrangement than on the preceding segments. Gland spines of the marginal fringe in the normal positions occurring singly or in pairs of unequal lengths except in one species. Prepygidial abdominal segments with

groups of gland tubercles in the usual positions. Perivulvar pores wanting. Anal orifice situated towards the base of the pygidium.

Scale of adult female pyriform, convex and white with terminal exuviae; male scale white, with subparallel sides, uncarinated or with the median carina faintly indicated.

Notes.

In addition to the genotype, *dura* Newstead, *reticulata* Malenotti, *distincta* Leonardi and *kirkianae* Hall are assigned to the genus. All five species have been found in S. Rhodesia and three of them—*dura*, *mashonae* and *kirkianae*—on *Uapaca* (EUPHORBACEAE). *Ledaspis reticulata* is known also from Italian Somaliland and Kenya, *distincta* from S. Africa and *dura* from Uganda. This gives a wide distribution throughout eastern and southern Africa.

Ledaspis belongs to the group of genera of the *Phenacaspis* complex, from all of which it differs in lacking perivulvar pores. It appears to come closest to *Tecaspis*. *Ledaspis distincta* is certainly a discordant element, but fits in better here than elsewhere. The species may be said to fall into two groups. Group *distincta*, in which the gland spines of the pygidial fringe are arranged in groups of about 7 spines with the exception of the group in the 1st interlobular space, which consists of 4. The median lobes are large and prominent. Group *mashonae*, in which the corresponding groups of gland spines usually consist of 2 spines of unequal size. The median lobes are squat typically, but always smaller and less prominent than in *distincta* and of quite different form.

Ledaspis dura was placed by MacGillivray (1921: 361) in *Asymmetraspis* MacGillivray, but it bears little resemblance to *distorta* Newstead, the type of that genus, and the two species are clearly not congeneric. All the five species, as well as nine others, have at various times been placed in the genus *Dinaspis*, a genus, it is now recognised, with which they have nothing to do.

Malenotti described *Dinaspis reticulata* var. *minor* from the Italian Somaliland on *Balanites somalensis*. A single slide of this species—presumably from the type material as it carries identical data—has been available, but is not sufficiently good to enable the characters to be made out satisfactorily. Some material collected on *Balanites* sp. in Kenya by Professor P. A. Buxton was typical *reticulata* Malenotti.

The five included species may be separated as follows:—

1. Sclerotised dermis of the anterior half of the body with a clearly reticulated pattern *reticulata* Malenotti.
- Dermis lacking such reticulated dermal pattern 2.
- 2(1). Gland spines of the pygidial fringe arranged in groups of about 7 spines with the exception of the group in the 1st interlobular space, which consists of 4. Median lobes large and prominent. Second lobes duplex, the inner lobules well developed and pointed, the outer lobules, if present, small and inconspicuous *distincta* Leonardi.
- Never more than two spines in the corresponding groups. Median lobes often squat, broader than long, but may be prominent and relatively large. Second lobes duplex, small and inconspicuous 3.
- 3(2). Median lobes prominent, about as broad as long, never definitely broader than long; dorsal pores on the 6th segment few, often absent altogether and never exceeding 6 *dura* Newstead.
- Median lobes not prominent, squat and definitely broader than long; dorsal pores on the 6th segment always more than 6 in number 4.
- 4(3). Median lobes with a conspicuous acute projection on the basal half of the inner margin; gland spines marginally of segment 4 on either side numerous—usually about 8. Female at maturity large, up to 3 mm. in length *mashonae* Hall.

Median lobes with no conspicuous inner projection; with only 2 gland spines marginally of segment 4; female at maturity not exceeding 2 mm. in length *kirkianae* Hall.

Genus *Lepidosaphes* Shimer.

Several African species have been referred to this genus, but only three of those that have been seen are accepted here. Two of these are well-known species of world-wide distribution, but the third, *sacchari* Hall, described from Egypt, is retained in the genus with some hesitation. Material of this species was received from Sierra Leone on *Chasmodon caudatum* (Gramineae).

Lepidosaphes sacchari differs from a typical *Lepidosaphes* in not having clearly developed duplex lobes, the outer lobule being, if present at all, extremely poorly represented, in the nature of the gland spines of the marginal fringe and the widely separated median lobes.

Ferris (1941: 300) erected a genus *Nilotaspis* for the reception of *Coccomytilus halli* Green, described from Egypt, and in his notes on the new genus stated that *Lepidosaphes bicuspis* Hall, *Coccomytilus isis* Hall and *C. retamae* Hall, all described from the same country, seemed to be candidates for admission to the genus. In the opinion of the author, *bicuspis* and *isis* should be transferred to *Nilotaspis*, but *retamae* differs from the type species and the two others referred to in having the dorsal pores on the pygidium scattered, and the pores on the prepygidial segments confined to the marginal region.

Lepidosaphes sacchari resembles a *Nilotaspis* in some respects, but differs in having lateral spurs on the 3rd and 4th segments, a second pair of pygidial lobes and gland tubercles, rather few and small though they may be, on the prepygidial segments. This and the other four species above referred to, all described from Egypt, have undoubtedly a general resemblance and may subsequently be included in the genus *Nilotaspis* when more is known about *Lepidosaphes* and allied genera. For the time being it is considered advisable to retain *sacchari* in *Lepidosaphes*.

The three included species may be separated as follows:—

1. Prepygidial abdominal segments with secondary lobes or spurs at each anterior angle; dorsum may or may not be sclerotised but without small sclerotised bosses near the lateral margins on the 1st, 2nd and 4th abdominal segments 2.
- Prepygidial abdominal segments without secondary lobes or spurs at each anterior angle; dorsum not sclerotised but with small sclerotised bosses near the lateral margins on the 1st, 2nd and 4th abdominal segments *beckii* Newman.
- 2(1). Abdominal segments 2 to 4 with sclerotised marginal spurs at each anterior angle; dorsum of the thoracic area and 1st abdominal segment rather heavily sclerotised; gland spines between the median lobes not extending beyond the apices of the lobes; second lobes strongly duplex; gland spines at the base of the pygidium relatively long and conspicuous *gloverii* Packard.
- Abdominal segment 2 never with a sclerotised spur, segments 3 and 4 with spurs, though sometimes small and inconspicuous, particularly on segment 3; dorsum at most with the merest trace of sclerotisation; gland spines between the median lobes long, at least twice as long as the lobes which are rather widely separated; outer lobule of second lobes, if present, very poorly developed and inconspicuous; gland spines at the base of the pygidium small and inconspicuous

sacchari Hall.

Genus *Leucaspis* Targioni.

Represented by a single species—*L. cockerelli* (de Charmoy)—recorded from Tanganyika on palms by Lindinger (1913 : 79).

Genus *Marchalaspis* MacGillivray.

This genus was erected for a single species—*Chionaspis vuilleti* Marchal (1909 : 175)—described from French Guinea on *Copaifera guibourtiana*?. It has not been seen, but from the original description it appears to be a striking form for which the erection of a new genus was justified.

Genus *Mitulaspis* MacGillivray.

Genotype :—*Chionaspis funtumiae* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body fusiform with abdominal segments 2, 3 and 4 having their lateral margins produced and each with a conspicuous spine-carrying process anteriorly. Pygidium with an elongate median sclerotised pattern, broadly rounded, with three pairs of lobes; median pair large, obconical, widely separated but not yoked, with a pair of gland spines and one or two marginal pores between them; second lobes duplex, of the same shape as the median lobes but smaller, and the outer lobule smaller than the inner; third lobes smaller, duplex but outer lobule inconspicuous. Gland spines of the second and third interlobular spaces in pairs; posterior to the third lobes there are two groups each consisting of three spines. Dorsal pores scattered, each pore encircled by a narrow band of sclerotised tissue. Marginal areas as far as the mesothoracic segment with relatively numerous pores and groups of gland tubercles in the usual positions. Perivulvar pores wanting. Anal orifice situated near the base of the pygidium.

Scale of the adult female opaque white, moderately convex, rather broadly dilated posteriorly with terminal exuviae. Male scale white, slightly wider about the middle or very narrowly pyriform, uncarinated.

Notes.

This genus was erected for a single species with very distinctive characters—*Chionaspis funtumiae* Newstead—described from Uganda on *Funtumia latifolia*. Recently the author was surprised to come across material of an undescribed species from Malaya on *Cinnamomum zeylanicum* that is not only congeneric with *funtumiae* but extremely close to it. It will be interesting to see if other species are discovered, and, if so, where and on what host plants.

Genus *Moraspis* gen. n.

Genotype :—*Chionaspis euphorbiae* Brain (figs. 15, 47).

Diagnosis.

Referable to the tribe Diaspidini. Body elongate oval and heavily sclerotised at maturity anterior to the second free abdominal segment. Pygidium broadly rounded with two pairs of inconspicuous lobes; median pair small, divergent and acutely rounded apically, with their bases clearly yoked together and a rather deep U-notch separating them; second lobes duplex, small with lobules apically rounded. Margin with a strikingly regular and more or less continuous row of marginal pores; in some places these may be two deep. Dorsal pores of the same size as the marginal pores; arranged in definite series as far as the 5th segment. Submedian and submarginal series present on the 6th segment but poorly developed. Metathoracic and free abdominal segments with irregular lines of similar pores

extending from margin to margin; in the marginal areas the pores are more numerous and scattered. Gland spines of the pygidial margin occurring singly, four in number either side of the median lobes. Gland tubercles on free abdominal segments wanting. Perivulvar pores present. Anal orifice situated towards the base of the pygidium.

Scale of adult female white, pyriform, moderately broadened posteriorly, and finely striated transversely. Male scale white and uncarinated or obscurely carinated.

Notes.

This genus falls within the complex of genera of the *Phenacaspis* type, which is so strongly developed in the Ethiopian region. It is characterised by the quite abnormal development of marginal pores, the lack of gland tubercles on the abdominal thoracic segments, and the extremely dense sclerotisation of the anterior two-thirds of the body.

So far only the type species, described from S. Africa on *Euphorbia*, is known.

Genus *Nelaspis* gen. n.

Genotype :—*Chionaspis exalbida* Cockerell.

Diagnosis.

Referred to the tribe Diaspidini. Body broadly fusiform with membranous dermis. Pygidium broadly rounded with rather indefinite characters. Median lobes small and inconspicuous, set well apart and neither zygotic nor yoked basally; gland spines and marginal pores between the median lobes wanting. Second lobes small, single in the type species and inconspicuous, of much the same size as the median lobes. Marginal and submarginal pores of the 6th, 5th and part of the 4th segments conspicuously larger than the dorsal pores of the submedian groups and of all pores anterior to the 4th segment. Submedian groups clearly separated from the pores of the submarginal region; the former occur as far as the 6th segment, the latter to the 5th segment only. Marginally the pores occur as far as the mesothorax. Gland tubercles apparently wanting. Pygidial gland spines, small and inconspicuous, occurring singly in the usual positions. Perivulvar pores present. Anal orifice situated about the middle of the pygidium.

Scale of adult female white, elongate, broadened posteriorly. Male scale white, with subparallel sides and a distinct median carina.

Notes.

This genus belongs to the group of typically Ethiopian genera in which the median lobes are small and widely set apart. It is characterised by the indefinite nature of the characters of the pygidial fringe, the well-defined submedian groups of dorsal pores of a much smaller size than those of the marginal and submarginal regions of segments 4 to 6.

In addition to the type species, *Chionaspis humilis* Brain is included. Both occur on *Aloe* and are so close that it is not easy to give satisfactory characters for their separation. Authentic material of the two species from S. Africa supports the view that, although the two are very closely allied, they are distinct. They may be separated as follows :—

1. Pygidial lobes small but clearly visible; median lobes usually strongly divergent with a shallow indentation of the margin between; second lobes duplex *humilis* Brain (figs. 17, 49).
- Pygidial lobes small and very inconspicuous; median lobes not strongly divergent and margin between not noticeably indented; second lobes single *exalbida* Cockerell (figs. 16, 48).

Genus *Operculaspis* Laing.

Represented by a single species—the type species, *O. crinitus* Laing—described (1925 : 63) from Tanganyika on a forest tree. This species is of most unusual form. Laing, in erecting a new genus for its reception, regarded it as belonging to the Aspidiotini as “its affinities are entirely with such genera as *Selenaspidus* and *Pseudacmidea*.” Ferris (1937a : 5) stated that it belonged, in his opinion, to the Diaspidini rather than to the Aspidiotini, as it possessed gland spines and the ducts seemed to be more nearly of the Diaspidine than of the Aspidiotine type. The author prefers for the present to leave the question open. *Morganella longispina* (Morgan) and *M. conspicua* (Brain) both have plates or gland spines supplied by microducts, and the dorsal ducts in *O. crinitus* are at most only obscurely two-barred. In the larval form also the two enlarged ducts on the dorsal side of the head so characteristic of the larvae in Diaspidini are wanting.

Genus *Parlatoria* Targioni.

Seven species of this genus are known from the Ethiopian region. Of these five have a world-wide distribution and have almost certainly been introduced. Only two have been described from Africa: *blanchardii* Targioni from Egypt, and *fluggeae* Hall from S. Rhodesia. The first of these is now known to occur far beyond the confines of Egypt and may not be of African origin. *Parlatoria fluggeae*, described from S. Rhodesia, is not known from elsewhere at present, but as the genus appears to be Oriental in origin it is possible that even this species is not really native to Africa. Lindinger (1936 : 151) sank *fluggeae* as a synonym of *oleae* Colvee but Morrison (1939 : 15) disagreed with this view and later McKenzie (1945 : 64), in a revision of the genus *Parlatoria*, accepted *fluggeae* as a distinct species.

There is a slide labelled *Parlatoria perpusilla* Mask. in the collections of the British Museum which was presented by Prof. Cockerell and presumably determined by him. It appears from the label to have been sent to him from Natal by the late Claude Fuller. Unfortunately the preparation is in very poor condition, and as there is no other record of the species from Africa it is omitted here. It may be noted that some later workers have assigned this species to the genus *Gymnaspidis* Newstead.

The seven species may be separated by the following key :—

1. Lacking gland tubercles between the anterior spiracles and margin . . . 2.
- Gland tubercles always present between the anterior spiracles and margin . . . 3.
- 2(1). With a conspicuous lobe-like protuberance of the margin opposite the anterior spiracles; 4th pygidial lobe represented by a conspicuous sclerotised spur . . . *zizyphi* Lucas.
- With no trace of a lobe-like protuberance; 4th pygidial lobe wanting or not clearly differentiated . . . *blanchardii* Targioni.
- 3(1). Fourth pygidial lobe represented by a plate similar to but smaller than those on either side of it . . . *proteus* Curtis.
- Fourth lobe represented by a small sclerotised spur or rudimentary tubercle; never by a plate . . . 4.
- 4(3). With four plates between the 3rd lobe and rudimentary tubercle representing the 4th lobe; perivulvar pores in five groups . . . *oleae* Colvee.
- With three plates between the 3rd and 4th lobes; perivulvar pores normally in four groups . . . 5.
- 5(4). Plates between the 3rd and 4th lobes with broad bases tapering sharply apically; pygidial lobes broad and stout . . . *fluggeae* Hall.

- Plates between the 3rd and 4th lobes broad throughout and apically fringed; pygidial lobes slender 6.
- 6(5). With a small dermal pouch laterally of each posterior spiracle; dorsal pores in the submarginal region at the base of the pygidium relatively few *camelliae* Comstock.
- With no such dermal pouch laterally of each posterior spiracle; dorsal pores in the submarginal region at the base of the pygidium relatively numerous *pergandii* Comstock.

Genus *Phenacaspis* Cooley & Cockerell (figs. 64, 68, 72).

The genus *Phenacaspis* is recognised to be an Oriental genus, of which the principal characters are understood here to be as follows:—

The dermal tissues membranous or at least never strongly sclerotised with the exception of the pygidium. Median pygidial lobes, not prominent, longer than broad, divergent but with their bases definitely yoked together and with a notch between, causing them to appear sunken in the apex of the pygidium. The dorsal pores relatively large and arranged in regular segmentally arranged single rows interrupted to form submedian and submarginal series. The former present only to the 6th segment and the latter normally only to the 5th. Submedian series on abdominal segments 1 and 2 either wanting or very poorly developed. Perivulvar pores always present in five groups. Gland spines of the pygidial fringe arranged singly on segments 6, 7 and 8, 1 or 2 on segment 5, and 2 to 4 on segment 4.

One of the characteristics of the Ethiopian Diaspidini is the relatively high percentage of species in which the median lobes are more or less strongly yoked basally and for this reason several have been placed in the genus *Phenacaspis* in the past. In the author's opinion only two can be assigned to the genus—*dilatata* Green and *kenyae* Hall—the former being a species described from Ceylon and almost certainly introduced into Africa. Even *kenyae* differs from the genotype and is doubtfully placed because the gland spines occur in pairs in the interlobular spaces and the median lobes are not strongly divergent. The remaining 21 species fall into three more or less well-defined groups for which the genera *Rolaspis*, *Tecaspis* and *Voraspis* are erected (figs. 64–75). It is almost certain that many more species belonging to this complex of genera remain to be found in the future.

There are two slides of *P. inday* Banks in the collection of the Natural History Museum labelled 'on Date Palm leaf imported to Great Britain from South Africa', but there is no record of this species having been actually collected in S. Africa. *P. natalensis* Cockerell (1902: 25), described from Natal on Mango and recorded by Brain (1920: 100) also from Natal on Mango and Palm, is considered to be a synonym of *P. dilatata* (Green).

The two included species may be separated as follows:—

1. Median lobes strongly divergent; gland spines on segments 6, 7 and 8 arranged singly, 1 or 2 on segment 5 and usually 3 on segment 4
dilatata Green (figs. 64, 68, 72).
- Median lobes not strongly divergent; gland spines on segments 6, 7 and 8 arranged in pairs, 3 on segment 5, 6 or 7 on segment 4 . . . *kenyae* Hall.

Genus *Pinnaspis* Cockerell.

Many Ethiopian species have been assigned to this genus in the past and not a few of them quite wrongly. Four species are included here, of which one, *aspidistrae* var. *gossypii* Newstead, is raised to specific rank on the grounds that it possesses strongly developed dorsal scleroses anterior to the anal orifice,

median lobes relatively much larger, adult female itself larger and the female scale quite different in appearance from typical *aspidistrae*. It is actually very close to *marchali* Cockerell, of which, what is believed to be authentic material from the fruits of *Elaeis guineensis* from Dahomey has been compared with part of the type material of *gossypii* Newstead. The characters of the two species under the microscope are so much alike that no constant differences have been detected by which they can be separated. The scales of the adult female are, however, quite different, those of *gossypii* are very thin semitranslucent and pale brown, whilst those of *marchali* are white, neither so thin nor so semitransparent. Whether these differences are sufficiently constant to warrant considering the two species as distinct can only be determined by a better knowledge of the species of *Pinnaspis* occurring on Cotton and *Elaeis*. For the time being they are accepted as being distinct. *P. marchali* Cockerell is very close to *P. temporaria* Ferris (1942: 407) but in the latter species the scale of the adult female is said to be opaque white.

Another species which is also obviously very close but has not been seen is *Pinnaspis proxima* Leonardi. This may possibly prove to be the same as *P. marchali* Cockerell.

P. minor Maskell has been recorded by several authors from the Ethiopian region, but these must be misidentifications as Maskell's species is now believed to belong to another genus. This species is not recognised from the Ethiopian region, nor has *P. minor* var. *strachani* been seen.

The four included species may be separated as follows:—

1. Median lobes relatively large. Dorsal scleroses anterior to the anal orifice well developed. Lateral sclerotised bands on the pygidium with two oblique bars 2.
- Median lobes small or very small. Dorsal scleroses wanting or poorly developed. Lateral sclerotised bands lacking oblique cross bars but sometimes the one at the posterior extremity is poorly represented . . . 3.
- 2(1). Scale of adult female white, thin, and slightly semitranslucent
marchali Cockerell.
Scale of adult female pale brown, very thin and semitranslucent
gossypii Newstead (figs. 18, 50).
- 3(1). Median pygidial lobes not sunken; dorsal submarginal macroducts reduced in number, generally absent on the 5th segment and with one or two only on the 4th and 3rd segments; lateral extensions of metathoracic and 1st abdominal segments broadly rounded; scale of female white, very thin and translucent; male scales not known
buxi Bouché.
Median lobes appearing sunken; dorsal submarginal macroducts more numerous with at least 2 on the 5th segment and 3 or 4 on the 4th and 3rd segments; lateral extensions of metathoracic and 1st abdominal segments acutely rounded; scale of the female brown and rather thick; male scales white, tricarinate and usually abundant
aspidistrae Signoret.

Genus *Poliaspis* Maskell.

The tendency has been to assign any species to this genus which possesses supplementary groups of disc pores on the ventral dermis anterior to the normal groups of perivulvar pores. The result has been that in some cases virtually the only characteristic the species have in common is the presence of the supplementary groups of disc pores. Several African species show traces of such groups, in which they may be either not represented at all or indicated by the presence

of a few pores. Lindinger (1937), on the other hand, went to the other extreme and sank *Phenacaspis* Cockerell and *Asymmetraspis*, *Cooleyaspis*, *Duplachionaspis*, *Greenaspis* and *Versiculaspis* all of MacGillivray, as well as several other genera, as synonyms of *Poliaspis*, the spelling of which he emended to *Polyaspis*. This synonymy is rejected and the view is held here that the only species referable to the genus are those in which the characters, apart from the mere presence of supplementary pore groups, are congeneric with *P. media* Maskell, the type of the genus.

Five Ethiopian species have been assigned to *Poliaspis* in the past. In the author's opinion, not one of these is congeneric with *media* Maskell nor are they congeneric between themselves. Two at least are widely different from each other and the other three. Thus *parinari* Hall is placed in *Africaspis*, *argentata* Hall in *Inchoaspis*, *carissae* Cockerell in *Rolaspis* and *kiggelariae* Brain and *kiggelariae* var. *allophylli* Hall in *Tecaspis*. Morrison (1922: 88) considered *kiggelariae* Brain might be included in *Poliaspis*, but in the species in question the body is heavily sclerotised whereas in typical *Poliaspis* the body is membranous.

Genus *Protodiaspis* Cockerell.

MacGillivray (1921: 365) included in this genus *Chionaspis* (*Dinaspis*) *imbricata* Brain described from S. Africa on *Euclea natalensis*. This species has not been seen but it is almost certainly not referable to *Protodiaspis*. At the same time it is definitely wrongly placed in *Dinaspis*, but until the species is rediscovered it will not be possible to determine its correct generic position.

Genus *Pseudaulacaspis* MacGillivray.

The type species—*pentagona* Targioni—is the only representative of this genus known from the Ethiopian region. It occurs in S. Africa, S. Rhodesia, Tanganyika and Zanzibar.

Genus *Pseudoparlatoria* Cockerell.

Only the type species—*parlatorioides* Comstock—is known from the Ethiopian region. This was recorded by Lindinger (1910: 46) from Tanganyika on *Aristolochia* sp.

It is strongly suspected from the description and figure that *Diaspis tricuspidata* Leonardi (1914: 192) described from Nigeria is not only a species of *Pseudoparlatoria* but quite possibly *P. parlatorioides* Comstock.

Genus *Pudaspis* gen. n.

Genotype:—*Diaspis newsteadii* Leonardi (figs. 19, 51).

Diagnosis.

Referable to the tribe Diaspidini. Body circular, relatively large and membranous. Pygidium broadly rounded with a well-defined median sclerotic pattern and a single pair of large and prominent median lobes; these lobes are not zygotic but strongly sclerotised and with conspicuous inwardly directed basal sclerotisations. A pair of plate-like structures, which are shorter than the lobes, and a marginal pore present between the lobes. Immediately beyond the median lobes on either side is a similar short plate, the pygidial fringe between these plates and the base of the pygidium with several (about 15) conspicuous plate-like structures which are almost as long as the median lobes. Dorsal pores relatively small with short ducts. Submarginal and submedian groups usually well separated, the former occurring as far as the 6th segment but the latter not beyond the 5th segment.

The submarginal groups as far as the 1st segment consist of numerous pores, particularly on the free abdominal segments, and separate into two clearly defined series at a short distance from the margin. Gland tubercles, in the usual positions, relatively numerous. Perivulvar pores present in five sharply defined groups of numerous pores. Anal orifice situated towards the apex of the pygidium.

Scale of the adult female white, large, more or less circular and highly convex with subcentral sulphur-yellow exuviae. Male scale comparatively large, white, uncarinated and usually projecting away from the stem amidst a mass of fluffy white secretory matter.

Notes.

Only the type species at present known. This genus differs from *Diaspis* in having only a median pair of lobes, the marginal pores relatively small and no larger than the dorsal pores and the pygidial gland spines replaced by several conspicuous plate-like structures a pair of which (smaller) occur between the median lobes.

Genus **Rolaspis** gen. n. (figs. 66, 70, 74).

Genotype:—*Phenacaspis whitehilli* Hall.

Diagnosis.

Referable to the tribe Diaspidini. Body elongate, fusiform, often slightly sclerotised at maturity except intersegmentally. Median lobes more or less prominent, usually longer than broad with, typically, a V-shaped notch between and with their bases clearly yoked together. A pair of setae, but without gland spines or marginal pores, between the lobes. Second lobes duplex, well developed, the lobules rounded apically. Gland spines of the pygidial fringe, typically, arranged singly in the usual positions. Marginal and dorsal pores of the same size. Dorsal pores on segment 6 in a somewhat irregular submedian row, submarginal group lacking or represented by 3 or 4 pores at most, with a well-defined gap between the submedian series and submarginal group where represented. Dorsal pores on segments 1 to 5 arranged in more or less regular series and relatively numerous, especially in the marginal areas, often occurring right across segments 1 to 3, a few pores at least always present on one or more of these segments in the median area. Prepygidial and meta-thoracic segments with groups of gland tubercles in the usual positions. Perivulvar pores present in five groups. Anal orifice towards the base of the pygidium.

Scale of the adult female, white, elongate, broadened posteriorly with apical exuviae; male scale white, with apical exuvia, uncarinated.

Notes.

This genus differs from *Phenacaspis* in having some pores in the median region of segments 1 to 3, more numerous dorsal pores but less regularly arranged and median lobes more or less prominent and at most only slightly divergent. It differs from *Tecaspis* in the arrangement of the dorsal pores on segment 6, in having some pores in the median region of segments 1 to 3 and in having a well-developed pair of second lobes. In *Rolaspis* the median notch is generally V-shaped, the gland spines of the pygidial fringe arranged singly and the second lobes rounded apically, whereas in *Tecaspis* the median notch is generally U-shaped, the gland spines arranged in pairs and the second lobes are acute or acutely rounded.

Rolaspis differs from *Voraspis* in the nature of the median lobes and the arrangement of the dorsal pores.

Eight species, of which two are described below as new, in addition to the

genotype, are included in the genus *Rolaspis*. Of these *carissae* Cockerell and *munroi* differ from the genotype in having a U-shaped notch, but the shape of the notch has not been found to be a satisfactory character for generic separation. The former species also is more heavily sclerotised than is usual for the genus, whilst in the latter species the number of gland spines is more than usual. The species described as *Chionaspis chaetachmae* var. *imbricata* Hall is here raised to specific rank on the grounds that the pygidial gland spines are relatively longer, arranged singly and not in pairs, the dermis being somewhat sclerotised at maturity and in certain other respects. It is necessary, however, to give the species a new name because Brain earlier described a species *Chionaspis* (*Dinaspis*) *imbricata* from South Africa, and for that reason it is renamed here *spiculata*.

Type material of *lounsburyi* var. *ekebergiae* Brain has not been available for examination, but some material recently received on *Trichilia* sp. (MELIACEAE) from Durban has been identified as this species. *Ekebergiae* was described from specimens on *Ekebergia* sp. also belonging to the MELIACEAE from Durban. The specimens on *Trichilia* agree closely with Brain's description of *ekebergiae* and are certainly separable from *lounsburyi* Cooley, but as neither the type nor type material has been seen it is being retained as a variety. If the author's determination is correct *lounsburyi* var. *ekebergiae* is very close to *chaetachmae* also described from the same locality, and it may be that the two should be united.

The descriptions of the two new species are as follows :—

***Rolaspis compositae* sp. n. (figs. 22, 54).**

Scale of adult female silvery white, moderately convex, elongate and slender. Some individuals are more broadened posteriorly. Exuviae brown, the colour being somewhat obscured by a thin silvery white secretionary film. Ventral scale thin, usually persisting along the lateral margins.

Male scale white, with parallel sides, uncarinated.

Length of scale of adult female 2.5–3.5 mm., breadth 0.8–1.0 mm.

Body of adult female elongate, fusiform, membranous with margins of abdominal segments moderately produced. Antennal tubercle more strongly developed than usual with a single curved seta which is bifid at the base. Two to four parastigmatic glands associated with the anterior spiracles. Pygidium rounded with the fringe between the 5th and 6th and between the 6th and 7th segments rather deeply indented. Median lobes slightly divergent apically, rounded and coarsely serrated with a V-shaped notch between carrying a pair of minute setae, and with their bases yoked together by a sclerotic band. Second lobes duplex, the inner lobule being of much the same size and shape as the median lobe but not serrated apically; outer lobule separated from the inner, small and sharply pointed. Gland spines of the pygidial fringe well developed, occurring singly in the normal positions. Marginal pores having capitate heads carrying short microducts. Submedian groups of dorsal pores occurring as far as the 6th segment, submarginal groups not beyond the 5th. On the 3rd, 4th and 5th segments the submedian groups consist of two parallel and regular series, the same applies to the submarginal groups but it is less well marked. Pores occur marginally of all segments as far anterior as the mesothorax. On the 1st and 2nd abdominal and the metathoracic segments scattered pores of a somewhat smaller size occur, at intervals from margin to margin. Gland tubercles in well-developed groups in the usual positions. Perivulvar pores in five groups, median 2–6, anterior laterals 10–20, posterior laterals 18–30 (average of 15 examples 4 : 16 : 24). Anal orifice towards the base of the pygidium.

On slender twigs of a Composite plant (?*Senecio*), Prince Albert, Cape Province, coll. J. C. Faure and S. H. Skaife, 17.xi.17, S.N.2483. A heavy infestation in which the scales were arranged lying more or less regularly along the twigs.

***Rolaspis munroi* sp. n. (figs. 25, 57).**

Scale of the adult female glossy white, sometimes faintly striated transversely and with extraneous matter obscuring the glossy surface; moderately convex and broadened posteriorly. Exuviae brown. Ventral scale very thin, usually remaining adherent to the host plant.

Male scale white, more or less parallel sided, uncarinated.

Length of scale of adult female 2.5–3.0 mm.; breadth 1.0–1.25 mm.

Body of adult female fusiform with dermis faintly sclerotised at maturity. Antennal tubercle with one or two curved setae; where only one is present it is bifid at the base. A loose group of some 20 to 25 parastigmatic glands associated with each anterior spiracle. Margins of free abdominal segments not strongly produced laterally. Pygidium broadly rounded. Median lobes rather squat and flatly rounded, separated by a shallow U-shaped notch about $\frac{2}{3}$ the width of one, with a pair of small setae between and with their bases strongly yoked together. Second lobes duplex, small and inconspicuous, third lobes not clearly differentiated. Gland spines in groups of 3 to 5 spines except in the first interlobular space, where there are one or two and at the base, where there is a group of 6–8. On the ventral aspect of both segments 4 and 5 in a submarginal position is a group of about three very small gland tubercles. Marginal pores with an unusually long microduct carried by the capitate head. Dorsal pores of normal form, numerous, arranged in not very regular series and usually more or less continuous; on the 6th segment the submarginal portion of the series is generally wanting or poorly developed. Pores numerous in the marginal areas of all segments as far anterior as the mesothorax and, on abdominal segments 1 to 3, pores occur right across the segments at irregular intervals. The pores anterior to the 4th segment are rather smaller than those of the pygidium. Gland tubercles relatively numerous occur in groups in the usual positions. Perivulvar pores in five groups, median 2–7, anterior laterals 16–31, posterior laterals 25–48 (average of 16 examples 5 : 23 : 39). Anal orifice situated near the base of the pygidium.

On small twigs of native willow, Vryheid, Natal, coll. C. Fuller, 20.ix.05, No. S.N.2493 (Brain's No. 168); Kenhardt, Cape Province, coll. J. C. Faure, April 1917, S.N.2473.

This species is named after Mr. H. K. Munro, the well-known authority on the TRYPETIDAE, in recognition of his invaluable assistance in sending material of many of the S. African species dealt with in this paper.

The type specimens have been selected from the Natal material. The Cape Province material differs from that from Natal in several respects, but there does not seem to be sufficient justification to consider the forms as distinct in view of the close similarity existing between them. The Cape Province material differs in having only a small and comparatively compact group of parastigmatic pores, averaging about 5 pores, associated with the anterior spiracles, in having fewer gland spines on the pygidial fringe, the groups usually containing two and rarely more than three spines, and the series of pores on segment 6 extending much closer to the margin.

The capitate heads of the marginal pores in *munroi* carry unusually long fine microducts of the same type noted in *barhinnieae* Hall, *nigerensis* Vayssière and several other species. The presence of small gland tubercles on the ventral aspect of segments 4 and 5 in a submarginal position also occurs in *Denta-*

chionaspis margaritae (Brain) and is most strongly developed in *Versiculaspis diosmae* (Brain).

The only other species recorded from willow from Africa with which *munroi* might be confused is *Poliaspis kiggelariae* Brain, but it differs from that species in lacking the supplementary groups of disc pores, in having the tissues only faintly sclerotised at maturity, in having several gland spines in each group on the pygidial margin and in other respects.

The nine species included in *Rolaspis* may be separated by the following key:—

1. The notch between the median pygidial lobes U-shaped 2.
The notch between the median lobes V-shaped 3.
- 2(1). With supplementary groups of disc pores present on the ventral dermis anterior to the normal groups of perivulvar pores; anterior portion of the body strongly sclerotised; pygidial gland spines arranged singly; notch between the median lobes relatively deep; a small species, the adult female measuring 1.0–1.25 mm. on the slide
carissae Cockerell (figs. 20, 52).
Without such supplementary groups of disc pores; anterior portion of the body only moderately sclerotised at maturity; pygidial gland spines arranged in groups of 3 to 5; notch between the median lobes relatively shallow; adult female measuring 2.0–2.50 mm.
munroi sp. n. (figs. 25, 57).
- 3(1). Pygidial gland spines arranged singly 5.
Pygidial gland spines arranged in pairs 4.
- 4(3). Median pygidial lobes evenly and flatly rounded, not serrated apically; anterior portion of body membranous *chaetachmae* Brain (figs. 21, 53).
Median lobes finely serrated apically; anterior portion of body faintly but clearly sclerotised at maturity
lounsburyi var. *ekebergiae* Brain (figs. 24, 56).
- 5(3). Submedian groups of pores on the 3rd, 4th and 5th segments in two parallel and regular single rows; the same applies to the submarginal groups of pores but is not so clearly defined
compositae sp. n. (figs. 22, 54).
Submedian groups of pores on the 3rd, 4th and 5th segments arranged otherwise 6.
- 6(5). Pores on abdominal segments 2 and 3 numerous, extending in a somewhat irregular but more or less evenly spaced and unbroken line right across the segments; pores of a similar size to those in the series on the pygidium
spiculata new name for *chaetachmae* var. *imbricata* Hall (figs. 26, 58).
Pores on segments 2 and 3 extending right across the segments but not numerous and rather widely and irregularly spaced over the median section; pores on segment 2, and often on segment 3, of a clearly smaller size than those of the pygidial series 7.
- 7(6). Median lobes broader than long, squat, with indications of two or three notches on the inner margin; microducts to capitate heads of marginal pygidial pores extremely long *leucadendri* Brain (figs. 23, 55).
Median lobes prominent, not squat and more or less rounded apically and without notches on the inner margin; microducts of the marginal pores only moderately long 8.
- 8(7). Body of adult female large, measuring 2.5–3.0 mm. in length and 1.2–1.4 mm. in width on the slide with correspondingly large pygidium; median lobes not serrated apically; dorsal pores relatively numerous and on segment 6 the number in the submedian series is usually 11 and rarely as few as 8 *whitehillii* Hall (figs. 66, 70, 74).

Body of adult female smaller and narrower, measuring 1.75–2.0 mm. in length and 0.6–0.7 mm. in width on the slide with correspondingly smaller pygidium; median lobes finely serrated apically; dorsal pores fewer and on segment 6 the number in the submedian series is usually 4 and rarely as many as 8 *lounsburyi* Cooley.

Genus *Salaspis* gen. n.

Genotype :—*Chionaspis tenuidisculus* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body fusiform, much narrowed anteriorly, moderately sclerotised with a reticulated pattern. Anterior spiracles sunk in a definite shallow pit. Pygidium broadly rounded with two pairs of lobes, median lobes squat, broader than long, well separated by a shallow notch but not yoked together basally, with one or two conspicuous marginal pores between them and a pair of minute setae but no gland spines. Second lobes present, duplex; but outer lobule very small and inconspicuous. Gland spines simple, occurring singly. Marginal and dorsal pores of the same size, relatively few but rather large, surrounded by a ring of strongly sclerotic tissue, and in segmentally arranged rows except on segment 6, where the arrangement is not so definite. Marginal pores and gland tubercles on the prepygidial segments relatively few. Perivulvar pores wanting. Anal orifice towards the base of the pygidium. Medioventral area of the pygidium with several large oval longitudinally orientated vacuoles.

Scale of adult female small, convex, only slightly broadened posteriorly and flatly rounded at the posterior extremity. Male scale tricarinate.

Notes.

MacGillivray (1921 : 360) included *chionaspis tenuidisculus* Newstead and *C. dura* Newstead in the genus *Asymmetraspis*. The former is certainly not congeneric with *distorta*, the type of *Asymmetraspis*, nor is it congeneric with *dura*. At the same time, it probably comes closest to *Ledaspis* Hall, of which *dura* has been made the type. It differs from that genus in not having the median lobes definitely yoked together but in having a conspicuous marginal pore between them and several oval vacuoles medioventrally on the pygidium.

Genus *Scleromytilus* Hall.

This genus at present contains but a single species—*S. hargreavesi* Hall (1946 : 71)—described from Uganda on *Loranthus* sp.

Genus *Sclopetaspis* MacGillivray.

Genotype :—*Chionaspis laniger* Newstead.

Diagnosis.

Referable to the tribe Diaspidini. Body large, broadly fusiform with relatively short thoracic region. Anterior spiracles situated in shallow pits. Pygidium rounded, with indentations of the margin intersegmentally, with four pairs of lobes all dentate, median pair separated by a notch but not yoked and lacking gland spines or marginal pores between their bases; other lobes duplex and sharply pointed. Dorsal pores with short ducts numerous, arranged in series; on the 7th segment only the submarginal series is present, on the 6th both submedian and submarginal series are present and separate; anterior to this the series merge into one another. Large numbers of pores occur marginally of the 3rd and 4th segments, but anterior to these the pores become successively fewer as far as the anterior spiracles. Gland spines relatively small, occurring singly in the usual positions. Gland

tubercles apparently wanting. Perivulvar pores present. Anal orifice situated near the base of the pygidium.

Scale of adult female white, highly convex, broadening posteriorly, coarsely laminated transversely and with a felted woolly surface. Male scale not known.

Notes.

This genus at present contains only the type species. It is a genus with distinctive characters of doubtful affinities quite unlike any other recorded from the Ethiopian region.

Genus *Situlaspis* Ferris.

MacGillivray (1921: 389) erected a genus *Neosignoretia* with *Aspidiotus yuccae* Cockerell as type. Ferris (1937: 125) pointed out that *Neosignoretia* was quite erroneously referred to the Aspidiotini and united it with his *Situlaspis* in which he placed *yuccae* Cockerell. Amongst the species which MacGillivray assigned to *Neosignoretia* were *Aonidiella tectaria* (Lindinger), *Aspidiotus gowdeyi* Newstead and *Gymnaspsis africana* Newstead. Only the last named belongs to the Diaspidini. It is open to some doubt as to whether it is correctly placed in *Gymnaspsis* but it has certainly no resemblance to *Situlaspis*.

Genus *Syngenaspsis* Sulc.

MacGillivray assigned all the Ethiopian species of *Parlatoria* to this genus, with the exception of *sluggeae* Hall, which had not then been described. It is doubtful if the genus *Syngenaspsis* is separable from *Parlatoria*, but McKenzie (1945: 85) recognises it with some hesitation for the type species—*parlatoriae* Sulc—only, on the basis of the difference in body shape. The genus *Syngenaspsis* is not known to occur in the Ethiopian region, and the species referred to it by MacGillivray are here all placed in *Parlatoria*.

Genus *Tecaspis* gen. n. (figs. 67, 71, 75).

Genotype :—*Chionaspis* (*Phenacaspis*) *visci* var. *umtalii* Hall, which is here raised to specific rank.

Diagnosis.

Referable to the tribe Diaspidini. Body elongate, fusiform. Median lobes prominent, never appearing recessed and at most never more than slightly divergent; with their bases yoked and usually separated by a U-shaped notch. Second lobes usually present, duplex but small, acute or acutely rounded and often relatively inconspicuous. Dorsal pores arranged in regular segmentally arranged rows except on segment 6, where they are arranged in a group of more or less irregular shape, both submedian and submarginal groups being represented but not usually clearly separated. Pores numerous in the marginal and submedian regions on the prepygidial segments, but never occurring in the median area. Pygidial gland spines arranged singly in the genotype but normally in pairs. Groups of gland tubercles occurring in the usual positions. Perivulvar pores present in five groups and in addition supplementary groups may be present anterior to these. Anal orifice situated near the base of the pygidium.

Scale of adult female white, elongate, broadened posteriorly with terminal exuviae. Male scale white with terminal exuvia.

Notes.

Tecaspis comes closest to *Rolaspis*, the principal differences between the two genera being enumerated on p. 531. Eight species are assigned to the genus

in addition to the genotype. Of these the most discordant element is *sinoiae* but it is included because of the prominent nature of the median lobes, the poor development of the second lobes, which are acute apically, and the absence of dorsal pores in the median region of the prepygidial abdominal segments. *T. diplasia* Laing was originally described as a *Lepidosaphes*, but the absence of gland spines between the median lobes, the nature of the second lobes and other characteristics preclude its retention in that genus as understood here, and there seems no valid reason for excluding it from *Texaspis*.

Chionaspis tursioides Laing, in the author's opinion, is the same as *C. retigera* Cockerell, and the two species should be united under the latter name. The forms described as *Poliaspis kiggelariae* var. *allophylli* Hall and *Chionaspis visci* var. *umtali* Hall are considered to be distinct species and are raised to specific rank. Preparations from cotype material of *Chionaspis mytilaspiformis* Newstead show clearly the presence of three groups of supplementary disc pores, poorly developed though the groups may be.

The nine species included may be separated by the following key:—

1. With supplementary groups of disc pores on the ventral dermis anterior to the normal groups of perivulvar pores 2.
- Without such supplementary groups of disc pores 4.
- 2(1). Pygidial gland spines short, averaging $14\ \mu$, occurring singly; anterior portion of the body strongly sclerotised at maturity; dorsal pores on the 6th segment not clearly separated into submedian and submarginal groups *kiggelariae* Brain (figs. 27, 59).
- Pygidial gland spines arranged in pairs of spines of unequal lengths, the longer not averaging less than $20\ \mu$; anterior portion of the body only faintly sclerotised at maturity; dorsal pores on segment 6 may or may not be separated into submedian and submarginal groups 3.
- 3(2). Median lobes broader than long, having a somewhat squat appearance; dorsal pores on segment 6 separated into submedian and submarginal groups; with only 3 groups of supplementary pores; second lobes, if present at all, very flatly rounded *mytilaspiformis* Newstead (figs. 28, 60, 60a).
- Median lobes prominent, about as broad as long; dorsal pores on segment 6 arranged in a continuous somewhat irregular shaped group; with 5 groups of supplementary pores; second lobes acutely rounded apically *allophylli* Hall.
- 4(1). Dorsal pores on segment 6 very few, submedian group consisting of 2 to 5 pores in a single row, submarginal group, if present at all, represented by a single pore *sinoiae* Hall.
- Dorsal pores on segment 6 never as few 5.
- 5(4). The sclerosis yoking the median lobes extended along the margin of the 7th segment and along part or all of the 6th *visci* Brain (figs. 29, 62).
- Sclerosis yoking the median lobes not so extended 6.
- 6(5). Pygidial gland spines short and inconspicuous; with a group of several rather large gland tubercles just posterior of each anterior spiracle *diplasia* Laing.
- Pygidial gland spines long and conspicuous; gland tubercles just posterior to the anterior spiracles, if present at all, represented by one or two tubercles only 7.
- 7(6). Notch between the median lobes V-shaped, inner lobule of second lobes rounded *subvisci* Hall.
- Notch U-shaped, inner lobule of second lobes conical 8.
- 8(7). Pygidial gland spines arranged singly; median lobes relatively large, about $28\ \mu$ broad, rounded and finely serrated apically; group of pores

on the 6th segment and submedian group on the 5th segment clearly separated *umtali* Hall (figs. 67, 71, 75).
 Pygidial gland spines arranged in pairs of unequal lengths; median lobes prominent but not large, about $17\ \mu$ broad; group of pores on the 6th segment and submedian group on the 5th segment not clearly separated *retigera* Cockerell (fig. 61).

Genus *Triaspidis* MacGillivray.

The type of this genus—*Lepidosaphes bicornis* Green—was described from Victoria, Australia, on *Eucalyptus*. MacGillivray, amongst several species which he assigned to the genus, included four species, all described from the Cameroons by Lindinger—*aberrans*, *crudiae*, *kamerunensis* and *meridionalis*. Unfortunately these species are only known from the original descriptions but whatever their correct generic position may be it seems clear that they are not congeneric with the genotype of *Triaspidis*.

Genus *Unachionaspis* MacGillivray.

The type species of this genus was described from Japan on Bamboo. MacGillivray included two S. African species in the genus, one *ambigua* Brain on Lilac, the other *globosus* Brain on *Euphorbia*. The first-named species is one of the few S. African species that has not been seen but it seems most unlikely that it is correctly assigned to *Unachionaspis*. *Chionaspis globosus* Brain, on the other hand, is certainly not referable to the genus and is here placed in *Dentaspis* MacGillivray.

Genus *Unaspis* MacGillivray.

Represented by a single species *U. citri* (Comstock) recorded from Sierra Leone by Laing (1929 : 480) and from French Guinea by Leonardi (1914 : 187). It is almost certainly an introduced species and, although it has been recorded from many parts of the world, is probably Oriental in origin.

Genus *Versiculaspis* MacGillivray.

Genotype :—*Chionaspis diosmae* Brain.

Diagnosis.

Referable to the tribe Diaspidini. Body elongate, fusiform, with faint sclerotisation of the dermis of the anterior half at maturity. Pygidium rounded, with two pairs of lobes; median lobes, separated by a conspicuous U-shaped notch, rounded apically, the base of each with an inwardly directed strongly sclerotised band, these bands are not fused and the lobes are not actually yoked at their bases; second lobes small and inconspicuous, consisting of a single apically rounded lobule. Pygidial fringe lacking gland spines. Marginal pores in the usual positions. Dorsal pores of a similar size to those of the margin, occurring in well-defined series on the 1st to 4th abdominal segments, on the 5th and 6th the normal series have supplementary parallel series containing fewer pores and on the 7th there is a submarginal group. Ventral aspect of the 5th abdominal segment with a group of some 10 unusually large and conspicuous gland tubercles, the 4th segment with a similar group, consisting of one or two large gland tubercles and several of very much smaller size; segments 3 to 1 inclusive with groups of very small gland tubercles. Perivulvar pores wanting. Anal orifice situated near the base of the pygidium.

Scale of adult female comparatively broad, moderately convex and silky in appearance with conspicuous growth lines. Male scale not known.

Notes.

This species falls within the complex of genera of the *Phenacaspis* type. It is characterised by the median lobes having strongly convergent basal sclerotic bands which are not fused to form a basal yoke, the development of conspicuous gland tubercles submarginally on the 5th abdominal segment replaced by tubercles of a much smaller size on the segments anterior to the 5th, the lack of pygidial gland spines and the presence of a submarginal group of pores on the 7th segment.

The presence of gland tubercles in a similar position on the 4th and 5th segments occurs in two other species—*Dentachionaspis margaritae* (Brain) and *Tecaspis munroi* Hall, both from S. Africa—but in these species they are very much smaller and less conspicuous. In other respects the three species are quite different.

Visci Brain has sclerotic bands at the bases of the median lobes rather similar to those found in *diosmae* but is otherwise quite different.

The genus *Versiculaspis* contains at present only the type species which was described from S. Africa on *Diosma crenata*.

Genus **Voraspis** gen. n. (figs. 65, 69, 73).

Genotype :—*Chionaspis carpenteri* Laing.

Diagnosis.

Referable to the tribe Diaspidini. Body elongate, fusiform. Pygidium rounded with two pairs of lobes. Median lobes small, squat, broader than long with serrated apices, separated by a marginal notch, but with their bases yoked together. A pair of setae between the lobes but without gland spines or marginal pores. Second lobes duplex, the inner lobule much larger than the outer and longer than broad. Gland spines of the pygidial fringe occurring singly. Marginal and dorsal pores of the same size. Dorsal pores in segmentally arranged rows interrupted on the 4th, 5th and 6th segments into submarginal and submedian series; the submarginal series on segment 6 reduced to 3 or 4 marginal pores. Segments 4 and 5 and sometimes 3 with a few supplementary pores arranged in irregularly parallel series. Prepygidial and thoracic segments with gland tubercles and rather numerous pores. Perivulvar pores present. Anal orifice towards the base of the pygidium.

Scale of adult female white, elongate, broadened posteriorly with terminal exuviae: male scale white, parallel sided, faintly tricarinate or uncarinated.

Notes.

This genus comes close to *Phenacaspis* Cockerell, from which it differs in having median lobes of characteristic squat shape and smaller dorsal pores less regularly arranged, but usually in two roughly parallel series on each segment. For the differences from *Rolaspis* and *Tecaspis*, see under *Rolaspis*, p. 531. In addition to the type species, *Chionaspis nigerensis* Vayssière (1912: 368) described from Upper Senegal and seen on the same host plant from Nigeria, and *Phenacaspis bauhiniae* Hall (1946: 65) described from Senegal on *Bauhinia rufescens* are here included. The type species was described from Uganda on an unknown plant. In both *nigerensis* and *bauhiniae* the marginal pores have long microducts arising from their capitate heads. These are difficult to detect except in freshly prepared well-stained specimens, and although it is suspected that the marginal pores of *carpenteri* are of similar structure it is not possible to be certain.

Chionaspis nigerensis and *Phenacaspis bauhiniae* are very close and the differences are mostly relative and not easily defined. The median lobes of

P. baruhinae are of rather different shape and relatively closer together, the dorsal pores are fewer and the pygidial gland spines relatively longer than in *C. nigerensis*.

Chionaspis usambarica Lindinger (1913: 76), described from Tanganyika on *Sideroxylon inerme*, would appear from the description to be closely allied to *carpenteri* and referable to this genus.

The three species may be separated as follows:—

1. Second lobes duplex with both lobules well developed and conspicuous; female scale white *carpenteri* Laing.
Second lobes duplex, small and inconspicuous, outer lobule if present extremely small; female scale silvery white 2.
- 2(1). Perivulvar pores numerous, median group 10, anterior laterals 26–32, posterior laterals 30–42 *nigerensis* Vayssière (figs. 30, 63).
Perivulvar pores less numerous, median 2–9, anterior laterals 12–21, posterior laterals 12–26 *baruhinae* Hall.

KEY FOR THE SEPARATION OF THE GENERA OF DIASPIDINI RECORDED FROM THE ETHIOPIAN REGION.

1. Adult female entirely enclosed within the exuvia of the preceding stage 2.
Adult female not so enclosed 5.
- 2 (1). Adult female having disc pores on one or more segments anterior to the usual perivulvar pores; body elongate; second-stage female with well-developed lobes, terminally serrated plates and macroducts *Leucaspis* Targioni.
Adult female with never more than the usual perivulvar pores, whether these be present or absent 3.
- 3 (2). Adult female with the median lobes strongly divergent and separated by a deep notch but yoked together basally *Fiorinia* Targioni.
Adult female with the median lobes, if present, neither strongly divergent nor separated by a deep notch 4.
- 4 (3). Pygidial margin of adult female produced into one or more long processes *Adistiflorinia* Targioni.
Pygidial margin not so produced; lobes present, in the known African species, with plates in the interlobular spaces *Gynnaspis* Newstead.
- 5 (1). Scale of the adult female always more or less circular; body of adult female circular or turbinate, never elongate except in *Aulacaspis*, where the prosoma is conspicuously swollen 6.
Scale of adult female of various shapes but always elongate, usually broadening posteriorly; body of adult female elongate and fusiform, pyriform or narrowly elongate in shape 18.
- 6 (5). Body of adult female elongate with prosoma swollen, distinctly wider than the postsoma and usually quadrate in form with more or less parallel lateral margins *Aulacaspis* Cockerell.
Body of adult female never elongate, but usually turbinate, or more or less circular in shape 7.
- 7 (6). Median pygidial lobes of adult female strongly zygotic 8.
Median lobes not zygotic 9.
- 8 (7). With a long strongly sclerotised process arising from the base of each median lobe; other lobes wanting; perivulvar pores wanting *Hulaspis* gen. n.
With no such sclerotised processes; second and third pairs of lobes present, duplex but small; perivulvar pores present *Pseudaulacaspis* MacGillivray.

- 9 (7). With a pair of either plates or gland spines between the median lobes 10.
Lacking plates or gland spines between the median lobes 15.
- 10 (9). Macroducts of the pygidial margin with the axes of their orifices
orientated transversely and with a sclerotised rim surrounding each
orifice 11.
Macroducts with their axes set longitudinally or diagonally and the
sclerotised rim, when present, similarly orientated 12.
- 11(10). Without perivulvar pores; prosoma heavily sclerotised at maturity;
gland spines laterally serrate *Genaparlatoria* MacGillivray.
With perivulvar pores; prosoma not sclerotised at maturity; gland
spines fimbriate or toothed *Parlatoria* Targioni.
- 12(10). Median lobes well separated with a fish-tail structure between them
formed by a forked gland spine *Pseudoparlatoria* Cockerell.
Without any such fish-tail structure 13.
- 13(12). Median lobes prominent, not sunken and without a notch between;
lateral lobes wanting or reduced to minute triangular projections;
with a pair of conspicuous scleroses arising either from the bases of
the median lobes or from the angle between them 14.
Median lobes sunken with a deep notch between; lateral lobes duplex,
well developed; scleroses lacking *Furchadaspis* MacGillivray.
- 14(13). Perivulvar pores present in 5 large groups; scleroses short, very
stout and inwardly directed, arising from the bases of the median
lobes; gland spines of the pygidial fringe plate-like and apically
trifurcate, the pair between the median lobes smaller but clearly
developed and of the same form *Pudaspis* gen. n.
Perivulvar pores wanting; scleroses long, club-shaped, divergent
with inner extremity knobbed, arising from the angle between the
median lobes; gland spines of the pygidial fringe well developed
and simple, the pair between the median lobes small and not clearly
of a glandular nature *Howardia* Berlese et Leonardi.
- 15 (9). Without a marginal macroduct between the median lobes; anterior por-
tion of the body strongly sclerotised with a lateral thoracic projection
on either side; second and third lobes without any trace of division
into lobules; perivulvar pores wanting *Ambigaspis* MacGillivray.
With a marginal macroduct between the median lobes; body mem-
branous, usually without any lateral thoracic lobes or projections;
second and third lobes, when present, clearly duplex; perivulvar
pores normally present. 16.
- 16(15). With a pair of small gland spines between the median pygidial lobes;
dorsal pygidial pores in well-arranged segmented rows as far only as
the 5th segment, posterior to the 5th segment only a single sub-
marginal pore anterior to the second lobe *Carulaspis* MacGillivray.
Without such a pair of small gland spines; dorsal pores never in well-
arranged segmental rows, usually scattered, and may be very few,
and occurring as far as the 6th or 7th segments 17.
- 17(16). Lateral lobes, if present, very poorly developed; basal scleroses of
the dorsal marginal setae of segments 6 and 7 rather conspicuously
enlarged; without conspicuous glandular tubercles on the pygidial
margin *Epidiaspis* Cockerell.
Lateral lobes well developed and duplex; with conspicuous glandular
tubercles on the pygidial margin *Diaspis* Costa.
- 18 (5). Scale of adult female small, varying considerably in form according
to situation; usually elongate and highly convex but may be oval
or even more or less circular and only low convex; body oval or
asymmetrical when fully developed with anterior half always more
or less sclerotised; median pygidial lobes clearly separated but

- with bases joined by a sclerotised band; second and third lobes, if present, poorly represented; perivulvar pores wanting 19.
- Scale of adult female normally larger or much larger and always definitely elongate and often broadened posteriorly; body characters not in the same combination 20.
- 19(18). Pygidial dorsal pores, though few, arranged in well-defined rows; without a marginal macropore between the median lobes; anal and genital apertures situated at the base of the pygidium
- Asymmetraspis* MacGillivray.
- Dorsal pores not arranged clearly in rows; with a macropore between the median lobes; anal and genital apertures situated about the middle of the pygidium *Bantudiaspis* Hall.
- 20(18). With small and inconspicuous median pygidial lobes set widely, often very widely, apart; second lobes often larger than the median lobes; median lobes may be conical, apically serrate or rounded; if a sclerotic band arises from the base of each lobe these are not usually yoked to form a definite band 21.
- Median lobes zygotic or if not zygotic, relatively large and not set widely apart; when the lobes are relatively small and not zygotic, clearly linked by a sclerotic band; second lobes rarely larger than the median lobes 24.
- 21(20). Submedian series of dorsal pores in well-defined groups as far as the 6th segment, the pores being of a much smaller size than those of the marginal and submarginal regions of segments 5 and 6. Characters of the pygidial fringe rather indefinite. Occurring on aloes
- Nelaspis* gen. n.
- Dorsal pores scattered or in well-defined series, rarely in groups, never strikingly smaller than the submarginal or marginal pores 22.
- 22(21). Body of adult female, when fully developed, unusually large with unusually large and broad pygidium; dorsal pores numerous, occurring as far as segment 6; on segment 6 the pores may or may not show some arrangement in series but on the segments anterior to this the pores are arranged in definite series *Inchoaspis* MacGillivray.
- Body of adult female not unusually large and may be quite small, with pygidium of corresponding dimensions; dorsal pores usually not numerous, those on the pygidium being either quite definitely scattered or in very definite rows 23.
- 23(22). Dorsal pygidial pores scattered, without any definite arrangement, into rows or series; lacking a definite notch between the median lobes; body of adult female quite small, not exceeding 1.25 mm. in length and often less than 1.0 mm., frequently globose with dermis membranous and usually delicate *Dentaspis* MacGillivray.
- Dorsal pores arranged in very regular series, submedian group on segment 6 consisting of from 2 to 6 pores in a single regular line; always with a more or less conspicuous notch between the median lobes; body of adult female of medium size, rarely as short as 1.25 mm. in length, never globose and with the anterior half moderately sclerotised at maturity *Dentachionaspis* MacGillivray.
- 24(20). Median pygidial lobes either zygotic or with their bases definitely yoked together by a sclerotic band 25.
- Median lobes neither zygotic nor with their bases yoked together 38.
- 25(24). Median lobes definitely zygotic 26.
- Median lobes not definitely zygotic but with their bases clearly yoked together by a sclerotic band 30.
- 26(25). Median lobes with inner margins straight throughout their entire length and in close apposition 27.

- Median lobes with their inner margins in close apposition over part only of their length or with their inner basal angles at least in close apposition 28.
- 27(26). Median lobes small; pygidial and prepygidial macroducts confined to the margin and to a very few in the submarginal series; segment 6 with marginal macroducts only *Pinnaspis* Cockerell.
- Median lobes large and comparatively prominent; macroducts relatively numerous and not so confined; segment 6 always with a submarginal group of pores *Gadaspis* gen. n.
- 28(26). Margin of the 6th and 7th segments with, in each case, 1 to 3 dentate projections associated with one or more highly sclerotised marginal macropores *Africaspis* MacGillivray.
- Margin of 6th and 7th segments without dentate projections associated with highly sclerotised marginal macropores 29.
- 29(28). Median lobes only represented and these often small and inconspicuous; pygidial gland spines small and inconspicuous; dorsal pores not arranged in definite segmentally arranged rows *Contigaspis* MacGillivray.
- Median lobes well developed; 2nd lobes always present and usually duplex; pygidial gland spines well developed; dorsal pores arranged in definite segmentally arranged rows *Chionaspis* Signoret.
- 30(25). With a small triangular process between the median lobes arising from the dorsal aspect of the margin. Median lobes tridentate, 2nd and 3rd lobes conical; all lobes strongly sclerotised. Dorsal pores few, small and scattered; marginal pores not occurring beyond the 5th segment. Body narrow and elongate with parallel sides *Finaspis* gen. n.
- With usually a well-developed U- or V-shaped notch between the median lobes but no small triangular process. Marginal pores always present as far as the 7th segment. Other characters different or not in the same combination 31.
- 31(30). With a single median transverse group of some 14 or 15 supplementary pores ventrally anterior to the normal groups of perivulvar pores. Second lobes as large if not larger than the median lobes. Body very narrow and elongate *Cooleyaspis* MacGillivray.
- Without supplementary disc pores, whether perivulvar pores are present or not. When supplementary disc pores are present they are in the usual small groups and not confined to a conspicuous transverse series. Second lobes always smaller than the median lobes 32.
- 32(31). Margin of pygidium with a practically continuous series of marginal macropores which may be two-deep in places; gland tubercles on prepygidial segments wanting. Body anterior to the 2nd abdominal segment very heavily sclerotised *Moraspis* gen. n.
- Margin of pygidium with normally arranged marginal macropores; gland tubercles on prepygidial segments always present. Anterior portion of the body may or may not be heavily sclerotised 33.
- 33(32). Perivulvar pores wanting. Anterior portion of body often heavily sclerotised *Ledaspis* gen. n.
- Perivulvar pores present. Anterior portion of body rarely heavily sclerotised 34.
- 34(33). Body excessively long and narrow. Median lobes prominent and strongly divergent with a conspicuous projection on the inner margin of each *Greenaspis* MacGillivray.
- Body never excessively long and narrow. If median lobes strongly divergent not prominent and never with a conspicuous projection on their inner margins 35.

- 35(34). Median lobes not prominent and strongly divergent. Dorsal pores always clearly separated into submedian and submarginal groups . . . 36.
- Median lobes prominent and not divergent, or at most only slightly so. Dorsal pores may or may not be divided into submedian and submarginal groups . . . 37.
- 36(35). Median lobes broader than long and squat; with a supplementary line of pores on segments 3, 4 and 5 in addition to the normal submedian series and anterior to them; submarginal group on segment 6 usually represented by one or two pores . . . *Voraspsis* gen. n.
- Median lobes longer than broad; pores of submedian series on segments 3, 4 and 5 in a single regular line: submarginal group on segment 6 wanting . . . *Phenacaspsis* Cockerell.
- 37(35). Segment 6 with a submedian group of pores arranged in a more or less regular line; submarginal group wanting or represented by 3 or 4 pores at most, and always with a well-marked interval between the submedian and submarginal group when present; dorsal pores distributed at irregular intervals right across the prepygidial segments; 2nd pygidial lobes well developed and rounded apically . . . *Rolaspsis* gen. n.
- Dorsal pores on segment 6 more numerous, in groups or series never in a regular single line of pores; submarginal group always present but usually not clearly separated off from the submedian group; median area of the prepygidial segments without dorsal pores; 2nd pygidial lobes usually poorly developed; 2nd lobes and the usual small prominences of the margin of the 6th and 7th segments usually acute or acutely rounded . . . *Tecaspsis* gen. n.
- 38(24). Margin of the pygidium with membranous, short, broad apically serrated or at least bifurcated processes, each process associated with a marginal macropore, in addition to the lobes and gland spines; a similar process and macropore occurs between the median lobes. Confined to bamboos . . . *Kuwanaspsis* MacGillivray.
- Margin without such processes . . . 39.
- 39(38). With a pair of gland spines between the median lobes . . . 40.
- Without gland spines between the median lobes . . . 47.
- 40(39). Median lobes with a marginal macropore between their bases . . . 41.
- Median lobes without such marginal macropore . . . 43.
- 41(40). Body extremely long and narrow with parallel sides; marginally of the 3rd abdominal segment on each side with 2 enlarged gland tubercles each supplied by 3 microducts . . . *Daraspsis* gen. n.
- Body fusiform without enlarged gland tubercles marginally of the 3rd segment . . . 42.
- 42(41). Pygidial lobes somewhat obconical; gland spines arranged in groups of 2 or 3; dorsal pores relatively numerous, scattered, of much the same size as the marginal pores; perivulvar pores wanting . . . *Mitulaspsis* MacGillivray.
- Pygidial lobes rounded; gland spines arranged singly; dorsal pores relatively few, scattered, of a markedly smaller size than the marginal pores; perivulvar pores present . . . one species of *Aonidomytilus* Leonardi.
- 43(40). Median lobes large, close together, with inner margins straight, diverging slightly apically before curving round to a long oblique outer margin; other lobes wanting or represented by small sharply pointed tubercles . . . 44.
- Median lobes otherwise; 2nd lobes well developed and usually duplex; 3rd lobes often present . . . 45.
- 44(43). Entire body anterior of about the 2nd abdominal segment very

strongly sclerotised; lateral margins of prepygidial segments with a deep indentation; perivulvar pores lacking; some of the pygidial gland spines broad, plate-like, with forked apices; bases of median lobes without conspicuous sclerotised processes. . . . *Scleromytilus* Hall.

Anterior portion of body not sclerotised; lateral margins of prepygidial segments without a deep indentation; perivulvar pores present; pygidial gland spines simple; bases of median lobes with one or more conspicuous sclerotised processes *Andaspis* MacGillivray.

- 45(43). Body oval, margins of free abdominal segments very little produced and without spurs; gland tubercles extremely few and inconspicuous; dorsal pores in well-arranged series, but submedian groups not occurring anterior to the 3rd segment; gland spines of pygidial fringe in groups of 2 to 5 spines; perivulvar pores wanting; pygidial lobes, small, obconical in shape *Balaspis* gen. n.

Body elongate fusiform; other characters different or not in the same combination 46.

- 46(45). Dorsal pygidial pores, even if few, arranged in definite segmented rows or series *Lepidosaphes* Shimer.

Dorsal pygidial pores distributed irregularly

some species of *Aonidomytilus* Leonardi.

- 47(39). Dorsum of pygidium with the sclerotisation forming a lattice-work pattern *Ischnaspis* Douglas.

Pygidium without a lattice-work pattern 48.

- 48(47). Median lobes squat with flatly rounded apically serrated margin with one or two conspicuous marginal macropores between them; ventral aspect of pygidium with irregularly arranged large oval vacuoles

Salaspis gen. n.

Median lobes of different shape, never with marginal macropores between them; pygidium without oval vacuoles 49.

- 49(48). Dorsal pygidial pores scattered or at most in very indefinite rows *Unaspis* MacGillivray.

Dorsal pores in well-defined rows or series 50.

- 50(49). Rarely with more than a very few, if any, dorsal pores on segment 7; dorsal pores relatively few; gland spines of the pygidial fringe usually occurring in pairs *Duplachionaspis* MacGillivray.

With usually a large submarginal group of pores on segment 7; dorsal pores numerous; gland spines of the pygidial fringe usually occurring singly 51.

- 51(50). With a conspicuous inwardly directed sclerotic band at the base of each median lobe; these bands are interrupted and not fused to form a yoke; with a group of relatively large gland tubercles submarginally on the ventral aspect of the 5th abdominal segment; without perivulvar pores *Versiculaspis* MacGillivray.

Without sclerotic bands arising from the bases of the median lobes; without a group of gland tubercles submarginally on the 5th segment; with perivulvar pores 52.

- 52(51). With median and 3 pairs of duplex lobes; all lobes prominent, sharply pointed and with coarsely serrated lateral margins

Sclopetaspis MacGillivray.

With median and one pair of duplex lobes only; all lobes broadly rounded, relatively squat and not prominent

Augulaspis MacGillivray.

LIST OF GENERA RECORDED FROM THE ETHIOPIAN REGION.

Genus	Genotype	Author	Generic characters or figures of genotype according to Ferris	Distribution within the Ethiopian Region
<i>Adicophorina</i>	<i>Flortinia secreta</i> Green	Leonardi, 1906 : 17, 52	1936 : 33	Tanganyika
<i>Africaspis</i>	<i>Diaspis chionaspiformis</i> Newstead	MacGillivray, 1921 : 307	1937a : 108	Widely distributed
<i>Ambraspis</i>	<i>Pseudomonidia lutei</i> Brin.	MacGillivray, 1921 : 394	1938a : 59	S. Africa
<i>Andaspis</i>	<i>Mytilaspis hawaiiensis</i> Maskell	MacGillivray, 1921 : 275	1937 : No. 3	S. Africa, S. Rhodesia, Tanganyika
<i>Anidiomyzaspis</i>	<i>Mytilaspis concolor</i> Cockrell	Leonardi, 1905 : 102	1937 : Nos. 5, 7	Gold Coast, Ivory Coast, S. Rhodesia
<i>Asymmetriaspis</i>	<i>Chionaspis distorta</i> Newstead	MacGillivray, 1921 : 311	—	S. Africa
<i>Aspiaspis</i>	<i>Chionaspis nudata</i> Newstead	MacGillivray, 1921 : 309	—	Tanganyika
<i>Astaspis</i>	<i>Aspidiotus</i> Bouché	Cockrell, 1892 : 180	1937 : Nos. 9, 10	Widely distributed
<i>Baleaspis</i>	<i>Baleaspis foveoli</i> sp. n.	gen. & sp. n. : 505, 506	—	S. Africa
<i>Bambiaspis</i>	<i>Houardia loranthi</i> Hall	Hall, 1941 : 225	—	S. Africa, S. Rhodesia
<i>Carulaspis</i>	<i>Aspidiotus juniperi</i> Bouché (= <i>Coccus vasci</i> Schrank)	MacGillivray, 1921 : 305	1937 : Nos. 11, 12	S. Africa
<i>Chionaspis</i>	<i>Coccus salicis</i> L.	Signoret, 1869 : 442	1936 : 42, 1937 : No. 13	Belgian Congo
<i>Coccomytilus</i>	<i>Mytilaspis convezus</i> Maskell	Leonardi, 1897 : 205	1941a : 15	Not represented
<i>Conigaspis</i>	<i>Chionaspis submunda</i> Newstead	MacGillivray, 1921 : 309	—	S. & S.W. Africa, S. Rhodesia
<i>Cooleyaspis</i>	<i>Chionaspis prasolonga</i> Newstead	MacGillivray, 1921 : 308	—	Uganda
<i>Coronaspis</i>	<i>Chionaspis coronifera</i> Green	MacGillivray, 1921 : 312	1937a : 8	Not represented
<i>Cryptodiaspis</i>	<i>Cryptodiaspis timuloides</i> Lindinger	MacGillivray, 1921 : 313	—	Cameroons
<i>Dacaspis</i>	<i>Cryptodiaspis concoloratus</i> Lindinger	Leonardi, 1906 : 909 : 26	—	French Guinea
<i>Dactyloaspis</i>	<i>Chionaspis capensis</i> Newstead	gen. n. : 511	1938a : 39	Widely distributed
<i>Dendachionaspis</i>	(= <i>Dinaspis lounsburyi</i> Leonardi)	MacGillivray, 1921 : 810	—	S. Africa, S. Rhodesia, Tanganyika, Uganda
<i>Dentaspis</i>	<i>Chionaspis substriata</i> Newstead	MacGillivray, 1921 : 312	1936 : 46	Widely distributed
<i>Diaspis</i>	<i>Diaspis calyptriformis</i> Costa (= <i>Aspidiotus echinocacti</i> Bouché)	Costa, 1928 : 7	1937 : Nos. 31, 36	S. Africa, S. Rhodesia, Tanganyika, Uganda
<i>Dinaspis</i>	<i>Dinaspis tcheri</i> Leonardi	Leonardi, 1911 : 282	1941 : No. 279	Not represented
<i>Duplichionaspis</i>	<i>Chionaspis graminis</i> Green	MacGillivray, 1921 : 307	1936 : 45, 1937 : No. 45	S. Africa, S. Rhodesia, Uganda
<i>Epidiaspis</i>	(= <i>Aspidiotus pirticola</i> del Guercio)	Cockrell, 1869 : 398	1937 : Nos. 49, 51	S. Rhodesia
<i>Finaspis</i>	<i>Lepidosaphes distivaca</i> Hall	gen. n. : 517	—	S. Rhodesia
<i>Furina</i>	<i>Furina pallida</i> (Lindinger)	Targioni, 1869 : 42	1937 : Nos. 54, 55	S. Africa, Tanganyika, Zanzibar
<i>Furchadaspis</i>	<i>Diaspis zamia</i> Morgan	MacGillivray, 1921 : 310	1937 : Nos. 58, 59	S. Africa, S. Rhodesia
<i>Gadaspis</i>	<i>Chionaspis (Pinnaspis) combrisi</i> Hall	gen. n. : 518	1937 : Nos. 60, 61	S. Rhodesia
<i>Gnapharioria</i>	<i>Parlatoria pseudaspidiotus</i> Lindinger	MacGillivray, 1921 : 248	1937 : Nos. 60, 61	Sudan
<i>Gnamptaspis</i>	<i>Chionaspis africana</i> Newstead	MacGillivray, 1921 : 309	1937 : Nos. 60, 61	S.W. Africa
<i>Gnamptaspis</i>	<i>Chionaspis elongata</i> Green	MacGillivray, 1921 : 307	1936 : 57	Italian Somaliland
<i>Gymnaspis</i>	<i>Gymnaspis neckmeze</i> Newstead	Newstead, 1868 : 92	1937 : Nos. 62, 63	S. Africa, Tanganyika, Uganda
<i>Hemichionaspis</i>	<i>Chionaspis aspidiotrae</i> Signoret	Cockrell, 1897 : 592	1936 : 59	= <i>Pannaspis</i> Cockrell
<i>Houardia</i>	<i>Chionaspis biclavata</i> Signoret	Bersee & Leonardi, 1898 : 347	1937 : Nos. 64, 65	Gold Coast, San Thomé, S. Africa, S. Rhodesia

LIST OF SPECIES RECORDED FROM THE ETHIOPIAN REGION.

Species name	Generic name	Author	Reference	Distribution records	Generic assign- ment by MacGillivray	Generic assignment adopted here
<i>aberrans</i>	<i>Lepidosaphes</i>	Lindinger	1909 : 83	Cameroons	<i>Triaspis</i>	Indeterminate
<i>africana</i>	<i>Chionaspis</i>	Newstead	1912 : 19	S. W. Africa	<i>Gramenaspis</i>	Type of <i>Gramenaspis</i>
<i>africana</i>	<i>Diaspis</i>	Newstead	1909 : 22	Cameroons	<i>Diaspis</i>	Apparently a <i>Diaspis</i>
<i>albans</i>	<i>Gymnaspis</i>	Newstead	1913 : 78	Tanganyika, Uganda	<i>Neosynuretia</i>	<i>Gymnaspis</i>
<i>alutophylli</i>	<i>Chionaspis</i> (<i>Poliaspis</i>)	Cockerell	1883 : 156	Gold Coast, Ivory Coast	<i>Coccomytilus</i>	<i>Acinomytilus</i>
<i>ambiguus</i>	<i>Chionaspis</i>	Hall	1929 : 374	S. Rhodesia	—	<i>Teaspis</i>
<i>ambiguus</i>	<i>Chionaspis</i>	Lindinger	1910 : 42		<i>Inchoaspis</i>	Type of <i>Inchoaspis</i>
<i>ambiguus</i>	<i>Chionaspis</i>	Brain	1920 : 97	S. Africa	—	<i>Henaspis dentatobis</i>
<i>argentea</i>	<i>Poliaspis</i>	Hall	1941 : 231	S. Rhodesia	<i>Unachionaspis</i>	Indeterminate
<i>asparagi</i>	<i>Chionaspis</i>	Laing & Cockerell	1929 : 1	S. Africa	—	<i>Inchoaspis</i>
<i>aspidistree</i>	<i>Chionaspis</i>	Signoret	1869 : 443	San Thomé, S. Africa, Tanganyika	<i>Hemichionaspis</i>	<i>Pinaspis</i>
<i>aspidistree gossypii</i>	<i>Hemichionaspis</i>	Newstead	1898 : 37	Uganda	—	= <i>Pinaspis gossypii</i>
<i>auratilis</i>	<i>Chionaspis</i>	Newstead	1920 : 204	Senegal	<i>Coronaspis</i>	<i>Dentachionaspis</i>
<i>bambusicola</i>	<i>Mytilaspis</i>	Cockerell	1898 : 44	Senegal	<i>Coccomytilus</i>	<i>Kuwanaspis</i>
<i>baphiae</i>	<i>Pyraclaspis</i>	Hall	1943 : 1	S. Rhodesia	—	<i>Afraspis</i>
<i>bautiniae</i>	<i>Poliaspis</i>	Hall	1946 : 65	Senegal	—	<i>Voruspis</i>
<i>beckii</i>	<i>Coccus</i>	Newman	1869 : 217	Widely distributed	<i>Lepidosaphes</i>	<i>Lepidosaphes</i>
<i>bertsei</i>	<i>Diaspis</i>	Malenotti	1916 : 347	Italian Somaliland	—	Certainly a <i>Dentachionaspis</i> , probably <i>D. tonsburyi</i>
<i>bertsei</i>	<i>Chionaspis</i> (<i>Pinaspis</i>)	Hall	1928 : 28	S. Rhodesia	—	<i>Afraspis</i>
<i>biclaris</i>	<i>Chionaspis</i>	Comstock	1888 : 98	Gold Coast, San Thomé, S. Africa, Rhodesia	<i>Hovareia</i>	<i>Hovareia</i>
<i>bicolor</i>	<i>Diaspis</i>	Laing & Laing	1932 : 63	Belgian Congo	—	<i>Diaspis</i>
<i>biobots</i>	<i>Gymnaspis</i>	Green & Laing	1923 : 130	Tanganyika	—	<i>Gymnaspis</i>
<i>bipindensis</i>	<i>Inchionaspis</i>	Lindinger	1909 : 32	Cameroons, French Guinea	<i>Inchionaspis</i>	Apparently an <i>Inchionaspis</i>
<i>blanchardii</i>	<i>Coccus</i>	Targioni	1869 : 32	Italian Somaliland	<i>Parlatoria</i>	<i>Parlatoria</i>
<i>boissacii</i>	<i>Diaspis</i>	Signoret	1869 : 432	Belgian Congo, S. Africa, Uganda	<i>Diaspis</i>	<i>Diaspis</i>
<i>brachydeipae</i>	<i>Lepidosaphes</i>	Hall	1928 : 276	S. Rhodesia	—	<i>Acinomytilus</i>
<i>brachydeipae</i>	<i>Coccus</i>	Kerner	1778 : 20, 52	Kenya, S. Africa	<i>Diaspis</i>	<i>Diaspis</i>
<i>bursii</i>	<i>Chionaspis</i>	Newstead	1911a : 171	French Guinea	<i>Phenacaspis</i>	Type of <i>Daraspis</i> gen. n.
<i>bursii</i>	<i>Aspidiotus</i>	Bouché	1851 : 111	Cameroons, Gold Coast, Tanganyika	<i>Pinaspis</i>	<i>Pinaspis</i>
<i>cacti</i>	<i>Diaspis</i>	Comstock	1883 : 91	S. Africa	<i>Diaspis</i>	= <i>Diaspis echinocacti</i>
<i>caffra</i>	<i>Chionaspis</i>	Brain	1920 : 346		<i>Dupluchionaspis</i>	<i>Afraspis</i>
<i>calianthina</i>	<i>Parlatoria</i>	Berlese et Leonardi	1932 : 20		<i>Synaspis</i>	= <i>Parlatoria oleae</i>
<i>calyptroides</i>	<i>Diaspis</i>	Comstock	1883 : 114		<i>Diaspis</i>	= <i>Diaspis echinocacti</i>
<i>canellulae</i>	<i>Parlatoria</i>	Comstock	1883 : 114		—	<i>Parlatoria</i>
<i>capensis</i>	<i>Chionaspis</i>	Newstead	1917 : 378	Belgian Congo, French Guinea	<i>Dentachionaspis</i>	Type of <i>Dentachionaspis</i>
<i>capparis</i>	<i>Chionaspis</i>	Brain	1919 : 233	S. Africa	<i>Dupluchionaspis</i>	Probably a <i>Dentachionaspis</i>
<i>cassiae</i>	<i>Diaspis</i>	Hall	1928 : 278	S. Rhodesia	—	<i>Diaspis</i>
<i>cassiae</i>	<i>Chionaspis</i> (<i>Poliaspis</i>)	Cockerell	1902 : 112	S. Africa	<i>Poliaspis</i>	<i>Poliaspis</i>
<i>carpenteri</i>	<i>Chionaspis</i>	Laing	1929 : 431	Uganda	—	Type of <i>Voruspis</i> gen. n.
<i>carueli</i>	<i>Diaspis</i>	Targioni	1869 : 43		<i>Caryaspis</i>	= <i>Caryaspis</i>
<i>cassiae</i>	<i>Chionaspis</i>	Newstead	1911 : 89		<i>Afraspis</i>	= <i>Afraspis chionaspiformis</i>
<i>chadachmoe</i>	<i>Chionaspis</i>	Brain	1919 : 235	S. Africa, S. Rhodesia	<i>Dupluchionaspis</i>	<i>Poliaspis</i>

LIST OF SPECIES RECORDED FROM THE ETHIOPIAN REGION—continued.

Species name	Generic name	Author	Reference	Distribution records	Generic assign- ment by MacGillivray	Generic assignment adopted here
<i>flava hawaitiensis</i>	<i>Mytilaspis</i>	Maskell	1894 : 47	S. Rhodesia	—	— <i>Andaspis hawaitiensis</i>
<i>fluggeae</i>	<i>Pantatoria</i>	Hall	1829 : 225	S. Africa	—	<i>Pantatoria</i>
<i>fulleri</i>	<i>Diaspis</i>	Cockerell	1829 : 225	Uganda	<i>Pseudaulacaspis</i>	<i>Aulacaspis</i>
<i>fundamine</i>	<i>Chionaspis</i>	Newstead	1914 : 310	S. Rhodesia	<i>Mitilaspis</i>	Type of <i>Mitilaspis</i>
<i>gibber</i>	<i>Chionaspis</i> (<i>Dinaspis</i>)	Hall	1929 : 372	French Guinea	—	<i>Dinaspis</i>
<i>giffardii</i>	<i>Dinaspis</i>	Leonardi	1914 : 215	French Guinea	—	Indeterminate, not <i>Dinas-</i> <i>pis</i>
<i>globosus</i>	<i>Chionaspis</i>	Brain	1919 : 236	S. Africa	<i>Unachionaspis</i>	<i>Dinaspis</i>
<i>glorerti</i>	<i>Coccus</i>	Packard	1869 : 527	San Thomé, Sierra Leone, S. Africa, Tanganyika, Uganda	<i>Lepidoaspis</i>	<i>Lepidoaspis</i>
<i>gossypii</i>	<i>Hemichionaspis</i>	Newstead	1908 : 37	Togoland	—	<i>Pinnaaspis</i>
<i>hamata</i>	<i>Diaspis</i> (<i>Cryptodiaspis</i>)	Lindinger	1909 : 28	Cameroon	<i>Cryptodiaspis</i>	<i>Cryptodiaspis</i>
<i>harpreavest</i>	<i>Chionaspis</i>	Labug	1825 : 61	Uganda	—	<i>Dinaspis</i>
<i>harpreavest</i>	<i>Scleromphitus</i>	Hall	1946 : 47	S. Rhodesia	—	Type of <i>Scleromphitus</i>
<i>hawaitiensis</i>	<i>Mytilaspis</i>	Maskell	1829 : 225	S. Africa	<i>Andaspis</i>	<i>Andaspis</i>
<i>habeola</i>	<i>Diaspis</i>	Labug	1829 : 65	B. Africa, Congo	—	<i>Diaspis</i>
<i>haridae</i>	<i>Chionaspis</i>	Graham	1896 : 132	S. Rhodesia	<i>Chionaspis</i>	<i>Aulacaspis</i>
<i>harmata</i>	<i>Chionaspis</i>	Brain	1919 : 231	S. Africa	<i>Phenacaspis</i>	<i>Nelaspis</i>
<i>harmata</i>	<i>Chionaspis</i> (<i>Dinaspis</i>)	Brain	1919 : 231	S. Africa	<i>Proctodiaspis</i>	Indeterminate, not <i>Proto-</i> <i>diaspis</i>
<i>inday</i>	<i>Chionaspis</i>	Banks	1906 : 222, 232, 787	S. Africa	<i>Phenacaspis</i>	<i>Phenacaspis</i>
<i>indigoferae</i>	<i>Chionaspis</i> (<i>Pinnaaspis</i>)	Hall	1928 : 286	S. Africa, S. Rhodesia	—	<i>Contigaspis</i>
<i>kamerunensis</i>	<i>Lepidoaspis</i>	Lindinger	1909 : 37	Cameroon, French Guinea	<i>Triaspis</i>	Indeterminate, not <i>Trias-</i> <i>pids</i>
<i>kenyae</i>	<i>Phenacaspis</i>	Hall	1946 : 66	Kenya	—	<i>Phenacaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i> (<i>Pollaspis</i>)	Newstead	1901 : 283	Tanganyika	<i>Adiosefernia</i>	<i>Phenacaspis</i>
<i>kygelariae allo-</i>	<i>Chionaspis</i> (<i>Pollaspis</i>)	Brain	1929 : 374	S. Africa	<i>Pollaspis</i>	<i>Phenacaspis</i>
<i>kygelariae phyti-</i>	<i>Chionaspis</i>	Hall	1929 : 374	S. Africa	—	— <i>Tecaspis allophyllis</i>
<i>kygelariae</i>	<i>Diaspis</i>	Hall	1941 : 227	S. Rhodesia	—	<i>Ledaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i>	Newstead	1920 : 206	Uganda	<i>Scopelaspis</i>	Type of <i>Scopelaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i>	Brain	1920 : 98	S. Africa	<i>Duplachionaspis</i>	<i>Rolaspis</i>
<i>kygelariae</i>	<i>Diaspis</i> (<i>Cryptodiaspis</i>)	Lindinger	1909 : 30	Cameroon	<i>Credodiaspis</i>	Type of <i>Credodiaspis</i>
<i>kygelariae</i>	<i>Diaspis</i>	Signoret	1882 : xxxv	Widely distributed	<i>Ischnaspis</i>	<i>Ischnaspis</i>
<i>kygelariae</i>	<i>Howardia</i>	Hall	1928 : 279	S. Africa, S. Rhodesia	—	Type of <i>Bombodiaspis</i>
<i>kygelariae</i>	<i>Diaspis</i>	Leonardi	1914 : 216	S. Africa, S. Rhodesia	—	<i>Dentachionaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i>	Cooley	1898 : 87	S. Africa	<i>Phenacaspis</i>	<i>Rolaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i> (<i>Phenacaspis</i>)	Brain	1920 : 99	S. Africa	<i>Phenacaspis</i>	<i>Rolaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i>	Newstead	1911a : 169	Gold Coast, Sierra Leone, Tan- ganyika	<i>Phenacaspis</i>	" <i>Chionaspis</i> ," see p. 508.
<i>kygelariae</i>	<i>Phenacaspis</i>	Brain	1919 : 210	S. Africa	<i>Ambigaspis</i>	Type of <i>Ambigaspis</i>
<i>kygelariae</i>	<i>Ischnaspis</i>	Labug	1932 : 67	Belgian Congo	—	<i>Ischnaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i>	Zehner	1898 : 1	Uganda	<i>Scopelaspis</i>	<i>Aulacaspis</i>
<i>kygelariae</i>	<i>Hemichionaspis</i>	Cockerell	1902 : 82	Dahomey, French Guinea	<i>Hemichionaspis</i>	<i>Phenacaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i>	Brain	1919 : 231	French Guinea	<i>Duplachionaspis</i>	<i>Dentachionaspis</i>
<i>kygelariae</i>	<i>Lepidoaspis</i>	Leonardi	1914 : 211	French Guinea	—	Indeterminate, not <i>Lepti-</i> <i>doaspis</i>
<i>kygelariae</i>	<i>Chionaspis</i> (<i>Dinaspis</i>)	Hall	1928 : 287	N. and S. Rhodesia	—	Type of <i>Ledaspis</i> gen. n.
<i>kygelariae</i>	<i>Lepidoaspis</i>	Hall	1931 : 288	S. Rhodesia	—	<i>Aonidomyllus</i>

meridionalis	Leptodaspidius	Lindinger	1909 : 88	Cameroons	Triaspis	Indeterminate, not Triaspis
minor strachani	Chionaspis	Maskell	1884 : 83	Several records	Hemichionaspis	Indeterminate
moorei	Hemichionaspis	Cooley	1899 : 84	W. Africa	Hemichionaspis	Presumably a Pinaspis
*munroi	Lepidosaphes	Doane & Ferris	1933 : 401	S. Africa	—	= Andaspis hawaiiensis
*mytilaspiformis	Rotaspis	sp. n.	1912 : 19	S. W. Africa	Duplacionaspis	Tecaspis
*natalensis	Chionaspis	Newstead	1896 : 390	S. Africa	Phenacaspis	Probably a Duplacionaspis
*natalensis	Phenacaspis	Maskell	1902 : 25	S. Africa	—	= Phenacaspis dilatata
*nigrescens	Coniostaspis	Cockerell	1914 : 190	S. Africa	—	Contaspis
*nigrescens	Diaspis	Leonardi	1912 : 368	S. Africa	Duplacionaspis	Type of Fudaspis gen. n.
*nigrescens	Chionaspis	Vayssière	1911a : 170	Nigeria, Senegal	Augulaspis	Type of Augulaspis
*oleae	Diaspis	Newstead	1880 : 89	Tanganyika	Augulaspis	Indeterminate
*olivina	Lepidosaphes	Colvée	1913 : 68	Sudan	Syngonaspis	Indeterminate, not Lepidosaphes
*pandani	Mytilaspis	Leonardi	1881 : 824	Eritrea	—	= Pinaspis buzi
*pachii	Chionaspis	Comstock	1916 : 351	Italian Somaliland	—	Duplacionaspis possibly D. asparagi Lalag & Cockrell
*parvianii	Poliaspis	Malenotti	1943 : 3	S. Rhodesia	Pseudoplatatoria	Africanaspis
*parvianii	Aspidiotus	Comstock	1883 : 64	Tanganyika	Diaspis	Apparently a Diaspis
*pallerosi	Diaspis	Maskell	1910 : 44	Tanganyika	—	Africanaspis
*pellucida	Pinaspis	Lindinger	1923 : 124	Gold Coast	—	= Fiorinia florivinae Targioni
*pentagona	Fiorinia	Targioni	1869 : 42	—	Pseudoleucaspis	Pseudoleucaspis
*pergandii	Diaspis	Targioni	1885 : No. 11	San Thomé, S. Rhodesia, S. Africa, Tanganyika, Zanzibar	Syngonaspis	Parlatoria
*pergandii	Parlatoria	Comstock	1881 : 327	Sierra Leone, S. Africa, Zanzibar	—	= Parlatoria camelliae
*pergandii	Parlatoria	Comstock	1883 : 114	S. Africa	Gymnaspis	Gymnaspis
*pergandii	Aspidiotus	Maskell	1897 : 299	S. Rhodesia	—	= Lepidosaphes beckii
*pinuspis	Aspidiotus (Diaspis)	Bouché	1851 : 111	Uganda	Cooleyaspis	Type of Cooleyaspis
*pinuspis	Chionaspis	Hall	1929 : 373	—	—	Parlatoria
*pinuspis	Chionaspis (Diaspis)	Newstead	1920 : 203	—	Syngonaspis	Parlatoria
*pinuspis	Aspidiotus	Hall	1928 : 289	S. Africa, Tanganyika	Hemichionaspis	Pinuspis
*proxima	Hemichionaspis	Curtis	1843 : 676	Dahomey, French Guinea, Nigeria, Portuguese W. Africa, Senegal, S. Africa	—	Genaparlatoria
*pseudaspidotus	Parlatoria	Lindinger	1905 : 131	Sudan	—	Indeterminate, not Dinaspis
*pseudomorphus	Diaspis	Leonardi	1914 : 218	French Guinea	—	Dentachionaspis
*pseudonivea	Chionaspis	Malenotti	1916 : 349	Italian Somaliland	Inciaspis	Type of Inciaspis
*pungonifera	Diaspis	Lindinger	1909 : 24	Cameroons	—	Andaspis
*pungonifera	Leptodaspidius	Lindinger	1920 : 500	Tanganyika	Inchoaspis	Inchoaspis
*pungonifera	Chionaspis (Diaspis)	Hall	1937 : 120	S. Rhodesia	Adiscoforinia	Adiscoforinia
*pygmaea	Fiorinia (Adiscoforinia)	Hall	1923 : 124	Tanganyika	Diaspis	Diaspis
*reuteri	Diaspis	Green & Lalag	1911 : 86	Uganda	—	Leaspis
*reticulata	Diaspis	Newstead	1916 : 343	Italian Somaliland, S. Rhodesia	—	Leaspis
*reticulata	Diaspis	Malenotti	1916 : 346	Italian Somaliland	—	Leaspis
*reticulata	Chionaspis (Diaspis)	Hall	1928 : 290	—	—	Leaspis reticulata Malenotti
*rethgera	Chionaspis	Cockerell	1901 : 249	S. Africa, Tanganyika	Duplacionaspis	Tecaspis
*rhusae	Howardia	Hall	1928 : 320	—	—	= Bantidiaspis loranthi
*rhusae	Diaspis	Brain	1913 : 225	—	—	= Furchaspis zamiae

LIST OF SPECIES RECORDED FROM THE ETHIOPIAN REGION—continued.

Species name	Generic name	Author	Reference	Distribution records	Generic assignment by MacGillivray	Generic assignment adopted here
* <i>richiei</i>	<i>Chionaspis</i>	Laing	1929 : 483	Sierra Leone, Tanganyika	—	<i>Dentichionaspis</i>
* <i>roseae</i>	<i>Aspidiotus</i>	Bouché	1834 : 14	Tanganyika	<i>Atulacaspis</i>	<i>Atulacaspis</i>
* <i>rugosa</i>	<i>Dentaspis</i>	Hall	1946 : 62	Uganda	—	<i>Dentaspis</i>
* <i>sachari</i>	<i>Lepidosaphes</i>	Hall	1923 : 23	Sierra Leone	—	<i>Lepidosaphes</i>
* <i>scutiae</i>	<i>Chionaspis</i>	Brail	1920 : 95	S. Africa	<i>Contignaspis</i>	<i>Africaspis</i>
* <i>senegalensis</i>	<i>Diaspis</i>	Vayssière	1914 : 206	Senegal	<i>Diaspis</i>	Apparently a <i>Diaspis</i>
* <i>sticticarpa</i>	<i>Diaspis</i>	Leonardi	1914 : 200	French Guinea	—	Indeterminate
* <i>sticticarpa</i>	<i>Homocarpus</i>	Leonardi	1914 : 187	French Guinea	—	Indeterminate, not <i>Homocarpus</i>
* <i>silvestrii</i>	<i>Ischnaspis</i>	Leonardi	1914 : 222	French Guinea	—	Indeterminate
* <i>sinicae</i>	<i>Chionaspis</i>	Hall	1928 : 281	S. Rhodesia	—	<i>Tecaspis</i>
* <i>somalensis</i>	<i>Coccomytilus</i>	Malenotti	1916 : 353	Italian Somaliland	—	Indeterminate, not <i>Coccomytilus</i>
* <i>spatulata</i>	<i>Diaspis</i>	Hall	1929 : 363	S. Rhodesia	—	<i>Diaspis</i>
* <i>spartinae natalensis</i>	<i>Chionaspis</i>	Maskell	1896 : 390	S. Rhodesia	—	<i>Diaspis</i> = ? <i>Duplacionaspis natalensis</i>
* <i>spiculata</i>	New name for <i>Chionaspis chalcidiae</i> var. <i>imbricata</i>	Hall	: 532	S. Africa, S. Rhodesia	—	<i>Rolaspis</i>
* <i>tanolophi</i>	<i>Chionaspis</i>	Cooley	1899 : 35	S. Africa, S. Rhodesia	<i>Chionaspis</i>	<i>Duplacionaspis</i>
* <i>terracae</i>	<i>Chionaspis</i>	Lindinger	1932 : 62	Belgian Congo	—	<i>Chionaspis</i>
* <i>stictica</i>	<i>Diaspis</i>	Lindinger	1909 : 25	Cameroon	<i>Diaspis</i>	Apparently a <i>Diaspis</i>
* <i>subnudata</i>	<i>Chionaspis</i>	Newstead	1912 : 19	S. and S.W. Africa	<i>Contignaspis</i>	Type of <i>Contignaspis</i>
* <i>subregularis spatulata</i>	<i>Diaspis</i>	Hall	1929 : 362	S. Rhodesia	—	<i>Diaspis</i>
* <i>subregularis spatulata</i>	<i>Diaspis</i>	Hall	1929 : 363	S. Rhodesia	—	<i>Diaspis spatulata</i>
* <i>substriata</i>	<i>Chionaspis</i>	Newstead	1910 : 197	Tanganyika, Uganda	<i>Dentaspis</i>	Type of <i>Dentaspis</i>
* <i>subtrici</i>	<i>Chionaspis</i>	Hall	1929 : 369	S. Rhodesia	—	<i>Tecaspis</i>
* <i>tangana</i>	<i>Phenacaspis</i> (<i>Phenacaspis</i>)	Lindinger	1910 : 45	Tanganyika	<i>Phenacaspis</i>	Possible a <i>Voraspis</i>
* <i>tegadensis</i>	<i>Chionaspis</i>	Zelnitner	1898 : 7	Tanganyika	—	<i>Atulacaspis</i>
* <i>tenax</i>	<i>Chionaspis</i>	Newstead	1920 : 202	Uganda	<i>Asymmetrionaspis</i>	Type of <i>Salaspis</i> gen. n.
* <i>tricuspidata</i>	<i>Lepidosaphes</i>	Lindinger	1909 : 19	Cameroon	<i>Lepidosaphes</i>	Indeterminate
* <i>tuberculata</i>	<i>Diaspis</i>	Leonardi	1914 : 192	Nigeria	—	Paralatoridea possibly P. paralatoridea
* <i>tuberculata</i>	<i>Chionaspis</i> (<i>Pinaspis</i>)	Hall	1929 : 368	S. Rhodesia	<i>Atulacaspis</i>	<i>Gadaspis</i>
* <i>tuberculata</i>	<i>Atulacaspis</i>	Newstead	1906 : 73	S. Rhodesia	—	<i>Atulacaspis chinamoni</i>
* <i>turnioides</i>	<i>Chionaspis</i>	Laing	1929 : 480	S. Rhodesia	—	<i>Tecaspis retigera</i> Cooke
* <i>uapacae</i>	<i>Chionaspis</i>	Laing	1929 : 480	S. Rhodesia	—	<i>Tecaspis retigera</i> Cooke
* <i>ugandae</i>	<i>Chionaspis</i>	Hall	1928 : 291	Uganda	—	<i>Ledaspis avara</i> Newstead
* <i>umlatii</i>	<i>Duplacionaspis</i>	Hall	1946 : 64	S. Rhodesia	—	<i>Duplacionaspis</i>
* <i>umla</i>	<i>Chionaspis</i> (<i>Phenacaspis</i>)	Lindinger	1929 : 370	S. Rhodesia	—	Type of <i>Tecaspis</i> gen. n.
* <i>usambarica</i>	<i>Chionaspis</i>	Lindinger	1910 : 43	Italian Somaliland, Tanganyika	—	<i>Africaspis chionaspis</i> (or <i>usambarica</i>)
* <i>usambarica</i>	<i>Chionaspis</i>	Lindinger	1913 : 76	Italian Somaliland, Tanganyika	—	Possibly a <i>Voraspis</i>
* <i>usambarica</i>	<i>Coccus</i>	Schrank	1781 : 296, 588	S. Africa	—	<i>Carulaspis</i>
* <i>usambarica</i>	<i>Chionaspis</i> (<i>Phenacaspis</i>)	Brail	1919 : 235	S. Africa	<i>Phenacaspis</i>	<i>Tecaspis</i>
* <i>usambarica</i>	<i>Chionaspis</i> (<i>Phenacaspis</i>)	Hall	1929 : 370	S. Africa, S. Rhodesia	—	<i>Tecaspis umlatii</i>
* <i>usambarica</i>	<i>Chionaspis</i> (<i>Phenacaspis</i>)	Hall	1929 : 370	French Guinea	<i>Marchalaspis</i>	Type of <i>Marchalaspis</i>
* <i>usambarica</i>	<i>Phenacaspis</i>	Marchal	1909 : 69	French Guinea	—	Type of <i>Rolaspis</i>
* <i>usambarica</i>	<i>Chionaspis</i>	Hall	1946 : 68	S. Africa	—	Type of <i>Furchadaspis</i>
* <i>usambarica</i>	<i>Diaspis</i>	Morgan	1890 : 44	S. Africa, S. Rhodesia	—	Type of <i>Furchadaspis</i>
* <i>usambarica</i>	<i>Coccus</i>	Lucas	1853 : xxviii	Belgian Congo, French Guinea, Gambia, S. Africa	<i>Parlatoria</i>	<i>Parlatoria</i>

* Either the "type" or what is believed to be typical or authentic material examined.

LIST OF SPECIES ARRANGED ACCORDING TO HOST PLANT GENERA.

It is hoped that most of the more important records have been included in the following list, but there may be a few that have been overlooked. Some have been purposely omitted where there appear to be good reasons to doubt the determinations. As the records have been derived from a variety of sources, the author cannot hold himself responsible for inaccuracies, whether they be of plant or insect, but it is believed that the list gives a reasonably accurate picture of the position so far as our present knowledge will permit.

The generic names follow those adopted in this paper, but where the species has not been actually seen the original author's generic name has been quoted, except in a few cases where there could be no doubt of its correct generic position.

ACANTHACEAE.

Asystasia.

Pseudaulacaspis pentagona (Targioni).

ACERACEAE.

Acer.

Diaspis boisduvalii Signoret.

Diaspis bromeliae (Kerner).

AMARANTACEAE.

Alternanthera.

Contigaspis cyanogena (Brain).

ANACARDIACEAE.

Lannea.

Africaspis chionaspiformis (Newstead).

Mangifera.

Aulacaspis cinnamomi Newstead.

Genaparlatoria pseudaspidiotus (Lindinger).

Phenacaspis dilatata (Green).

Pinnaspis proxima (Leonardi).

Pseudaulacaspis pentagona (Targioni).

Rhus.

Bantudiaspis lorantheri (Hall).

Furchadaspis zamiae (Morgan).

Gymnaspis faurei Brain.

Lepidosaphes florii Leonardi.

Rolaspis lounsburyi (Cooley).

Tecaspis mytilaspiformis (Newstead).

Schinus.

Pseudaulacaspis pentagona (Targioni).

ANNONACEAE.

Annona.

Pinnaspis proxima (Leonardi).

APOCYNACEAE.

Allamanda.

Pseudaulacaspis pentagona (Targioni).

Carissa.

Diaspis carissae Hall.

Diaspis subregularis Hall.

Rolaspis carissae (Cockerell).

Rolaspis spiculata (new name).

Funtumia.

Chionaspis lutea Newstead.

Mitulaspis funtumiae (Newstead).

Plumeria.

Diaspis boisduvalii Signoret.

Howardia biclavus (Comstock).

Pseudaulacaspis pentagona (Targioni).

Rauwolfia.

Africaspis pattersoni (Green & Laing).

ARACEAE.

Anthurium.

Parlatoria pergandii (Comstock).

Anubias.

Pinnaspis buxi (Bouché).

ARALIACEAE.

Cussonia.

Furchadaspis zamiae (Morgan).

ARISTOLOCHIACEAE.

Aristolochia.

Pseudoparlatoria parlatorioides (Comstock).

ASCLEPIADACEAE.

Calotropis.

Pinnaspis proxima (Leonardi).

BERBERIDACEAE.

Berberis.

Pseudaulacaspis pentagona (Targioni).

BIGNONIACEAE.

Bignonia.

Howardia biclavus (Comstock).

Pseudaulacaspis pentagona (Targioni).

Catalpa.

Pseudaulacaspis pentagona (Targioni).

Tecoma.

Pseudaulacaspis pentagona (Targioni).

BORAGINACEAE.

Heliotropium.

Pseudaulacaspis pentagona (Targioni).

BROMELIACEAE.

Ananas.

Diaspis bromeliae (Kerner).

Bilbergia.

Diaspis bromeliae (Kerner).

BUXACEAE.

Buxus.

Ischnaspis longirostris (Signoret).

Rolaspis carissae (Cockerell).

CACTACEAE.

Opuntia.

Diaspis echinocacti (Bouché).

CAPPARIDACEAE.

Cadaba.

Dentachionaspis berlesesi (Malenotti).

Capparis.

Africaspis chionaspiformis (Newstead).

Dentachionaspis capparisi (Brain).

Ledaspis reticulata (Malenotti).

Tecaspis retigera (Cockerell).

CAPRIFOLIACEAE.

Lonicera.*Howardia biclavis* (Comstock).

CARICACEAE.

Carica.*Howardia biclavis* (Comstock).*Pseudaulacaspis pentagona* (Targioni).

CELASTRACEAE.

Cassine.*Greenaspis elongata* (Green).*Elaeodendron*.*Tecaspis subvisci* (Hall).*Gymnosporia*.*Dentachionaspis lounsburyi* (Leonardi).

COMBRETACEAE.

Combretum.*Gadaspis combreti* (Hall).*Gadaspis excisa* (Hall).*Terminalia*.*Africaspis fici* (Newstead).

COMPOSITAE.

Senecio.*Rolaspis compositae* sp. n.

CONIFERAE.

Juniperus.*Carulaspis visci* (Schränk).*Thuja*.*Carulaspis visci* (Schränk).

CONNARACEAE.

Connarus.*Diaspis africana* Lindinger.

CORNACEAE.

Aucuba.*Ichnaspis longirostris* (Signoret).

CUCURBITACEAE.

Sphaerosicyos.*Phenacaspis dilatata* (Green).

CYCADACEAE.

Cycas.*Furchadaspis zamiae* (Morgan).*Encephalartos*.*Parlatoria proteus* (Curtis).

CYPERACEAE.

Cyperus.*Duplacionaspis paolii* (Malenotti).

DIPTEROCARPACEAE.

Monotes.*Africaspis chionaspiformis* (Newstead).

EBENACEAE.

Diospyros.*Africaspis diospyros* (Hall).*Euclea*.*Dinaspis imbricata* Brain.*Royena*.*Howardia biclavis* (Comstock).

EUPHORBIACEAE.

Aleurites.*Andaspis hawaiiensis* (Maskell).*Codiaeum*.*Lepidosaphes gloverii* (Packard).*Croton*.*Fiorinia floriniae* (Targioni).*Lepidosaphes beckii* (Newman).*Lepidosaphes gloverii* (Packard).*Parlatoria pergandii* Comstock.

EUPHORBIACEAE continued.

Cyclostemon.*Ichnaspis bipindensis* Lindinger.*Euphorbia*.*Balaspis faurei* gen. and sp. n.*Dentaspis globosus* (Brain).*Moraspis euphorbiae* (Brain).*Rolaspis whitehillii* (Hall).*Fluggea*.*Parlatoria fluggeae* Hall.*Hevea*.*Pseudaulacaspis pentagona* (Targioni).*Manihot*.*Aonidomytilus albus* (Cockerell).*Gymnaspis africana* Newstead.*Poinsettia*.*Howardia biclavis* (Comstock).*Pseudaulacaspis pentagona* (Targioni).*Ricinus*.*Aulacaspis fulleri* (Cockerell).*Pseudaulacaspis pentagona* (Targioni).*Sapium*.*Diaspis spatulata* (Hall).*Uapaca*.*Africaspis chipingae* Hall.*Dentachionaspis pittospori* (Hall).*Gadaspis tuberculata* (Hall).*Ledaspis dura* (Newstead).*Ledaspis kirkianae* (Hall).*Ledaspis mashonae* (Hall).

Genera unspecified.

Cryptodiaspis conservans Lindinger.

FAGACEAE.

Castanea.*Andaspis harviiensis* (Maskell).

FLACOURTIACEAE.

Kiggelaria.*Tecaspis kiggelariae* (Brain).

GERANIACEAE.

Geranium.*Pseudaulacaspis pentagona* (Targioni).

GRAMINEAE.

Andropogon.*Duplacionaspis stanotophri* (Cooley).*Bambusa*.*Kuwanaspis bambusicola* (Cockerell).*Chasmopodium*.*Lepidosaphes sacchari* Hall.*Cymbopogon*.*Duplacionaspis stanotophri* (Cooley).*Cynodon*.*Duplacionaspis asparagi* (Laing & Cockerell).*Eulalia*.*Duplacionaspis stanotophri* (Cooley).*Panicum*.*Duplacionaspis asparagi* (Laing & Cockerell).*Saccharum*.*Aulacaspis madiunensis* (Zehntner).*Aulacaspis tegalensis* (Zehntner).*Stenotaphrum*.*Duplacionaspis stanotophri* (Cooley).

Genera unspecified.

Aulacaspis herbae (Green).

GRAMINEAE continued.

Genera unspecified continued.

- Chionaspis natalensis* Maskell.
- Duplacionaspis stanotophri* (Cooley).
- Duplacionaspis ugandae* Hall.
- Rolaspis lounsburyi* (Cooley).

JUGLANDACEAE.

Juglans.

- Pseudaulacaspis pentagona* (Targioni).

LABIATAE.

Coleus.

- Lepidosaphes beckii* (Newman).

LAURACEAE.

Litsea.

- Aulacaspis cinnamomi* Newstead.

LEGUMINOSAE.

Acacia.

- Africaspis caffra* (Brain).
- Andaspis hawaiiensis* (Maskell).
- Aonidomytilus mazoeensis* (Hall).
- Coccomytilus somalensis* Malenotti.
- Dentacionaspis lounsburyi* (Leonardi).
- Pinnaspis aspidistrae* (Signoret).
- Pudaspis newsteadi* (Leonardi).

Baiea.

- Diaspis bicolor* Laing.
- Diaspis boisduvalii* Signoret.
- Diaspis helveola* Laing.

Baphia.

- Africaspis baphiae* Hall.

Baptisia.

- Andaspis hawaiiensis* (Maskell).

Bauhinia.

- Howardia biclavis* (Comstock).
- Voraspiis bauhiniae* (Hall).

Berlinia.

- Africaspis berliniae* (Hall).
- Aonidomytilus brachystegiae* (Hall).
- Coccomytilus chitinosus* Lindinger.

Brachystegia.

- Africaspis berliniae* (Hall).
- Aonidomytilus brachystegiae* (Hall).

Cassia.

- Africaspis chionaspiformis* (Newstead).
- Andaspis hawaiiensis* (Maskell).
- Contigaspiis naudei* sp. n.

Copaisfera.

- Marchalaspis vuilleti* (Marchal).

Crudia.

- Lepidosaphes crudiae* Lindinger.

Cynometra.

- Cryptodiaspis limuloides* Lindinger.
- Lepidosaphes aberrans* Lindinger.
- Lepidosaphes tenuior* Lindinger.

Erythrina.

- Andaspis hawaiiensis* (Maskell).
- Pseudaulacaspis pentagona* (Targioni).
- Gleditchia*.

- Pseudaulacaspis pentagona* (Targioni).

Indigofera.

- Contigaspiis indigoferae* (Hall).

Kennedya.

- Pseudaulacaspis pentagona* (Targioni).

Leucaena.

- Howardia biclavis* (Comstock).

LEGUMINOSAE continued.

Macrolobium.

- Cryptodiaspis hamata* Lindinger.
- Daraspis bussii* (Newstead).
- Ischnaspis macrolobii* Laing.
- Lepidosaphes meridionalis* Lindinger.

LILIACEAE.

Aloe.

- Dentacionaspis margaritae* (Brain).
- Nelaspis exalbida* (Cockerell).
- Nelaspis humilis* (Brain).

Asparagus.

- Duplacionaspis asparagi* (Laing & Cockerell).

Aspidistra.

- Pinnaspis aspidistrae* (Signoret).

Cordyline.

- Ischnaspis longirostris* (Signoret).

Dracaena.

- Ischnaspis longirostris* (Signoret).
- Phenacaspis tangana* Lindinger.

LOGANIACEAE.

Strychnos.

- Diaspis stilosa* Lindinger.
- Ischnaspis bipindensis* Lindinger.
- Ischnaspis longirostris* (Signoret).

LORANTHACEAE.

Loranthus.

- Bantudiaspis loranthi* (Hall).
- Diaspis parva* Lindinger.
- Diaspis subregularis* Hall.
- Lepidosaphes beckii* (Newman).
- Lepidosaphes kamerunensis* Lindinger.
- Scleromytilus hargreavesi* Hall.
- Sclopetaspis laniger* (Newstead).

Viscum.

- Carulaspiis visci* (Schränk).
- Inchoaspis dentilobis* (Newstead).
- Tecaspis visci* (Brain).

LYTHRACEAE.

Lagerstroemia.

- Andaspis hawaiiensis* (Maskell).

MALVACEAE.

Gossypium.

- Ischnaspis longirostris* (Signoret).
- Pinnaspis gossypii* (Newstead).

Hibiscus.

- Africaspis chionaspiformis* (Newstead).
- Pseudaulacaspis pentagona* (Targioni).

Sida.

- Pseudaulacaspis pentagona* (Targioni).

MARANTACEAE.

Maranta.

- Diaspis boisduvalii* Signoret.

MELIACEAE.

Cedrela.

- Pseudaulacaspis pentagona* (Targioni).

Ekebergia.

- Rolaspis lounsburyi* var. *ekebergiae* (Brain).

Khaya.

- Africaspis chionaspiformis* (Newstead).
- Diaspis senegalensis* Vayssière.

Melia.

- Africaspis chionaspiformis* (Newstead).

MELIACEAE continued.

Melia continued.*Aulacaspis fulleri* (Cockerell).*Trichilia*.*Howardia biclavis* (Comstock).*Ischnaspis longirostris* (Signoret).*Pinnaaspis buxi* (Bouché).*Rolaspis lounsburyi* var. *ekebergiae* (Brain).*Turraea*.*Africaspis chionaspiformis* (Newstead).*Bantudiaspis lorantheri* (Hall).*Xylocarpus*.*Chionaspis usambarica* Lindinger.

MORACEAE.

Ficus.*Africaspis chionaspiformis* (Newstead).*Africaspis communis* (Hall).*Africaspis fici* (Newstead).*Epidiaspis ficifoliae* Hall.*Morus*.*Pseudaulacaspis pentagona* (Targioni).

MUSACEAE.

Musa.*Phenacaspis dilatata* (Green).*Strelitzia*.*Pseudaulacaspis pentagona* (Targioni).

MYRTACEAE.

Callistemon.*Parlatoria pergandii* Comstock.*Eugenia*.*Andaspis hawaiiensis* (Maskell).*Psidium*.*Pseudaulacaspis pentagona* (Targioni).*Syzygium*.*Diaspis africana* Lindinger.

OLACACEAE.

Ximenia.*Voraspis nigerensis* (Vayssière).

OLEACEAE.

Jasminum.*Andaspis hawaiiensis* (Maskell).*Parlatoria oleae* (Colvée).*Ligustrum*.*Howardia biclavis* (Comstock).*Olea*.*Lepidosaphes olivina* Leonardi.*Syringa*.*Chionaspis ambiguus* Brain.

ONAGRACEAE.

Fuchsia.*Pseudaulacaspis pentagona* (Targioni).

ORCHIDACEAE.

Genera unspecified.

Diaspis boisduvalii Signoret.*Parlatoria pergandii* Comstock.*Parlatoria proteus* (Curtis).

PALMAE.

Borassus.*Fiorinia kewensis* Newstead.*Cocos*.*Pinnaaspis buxi* (Bouché).*Elaeis*.*Pinnaaspis marchali* (Cockerell).

PALMAE continued.

Hyphaene.*Dentachionaspis pseudonivea* (Malenotti).*Phoenix*.*Dentaspis substriata* (Newstead).*Fiorinia fioriniae* (Targioni).*Ischnaspis longirostris* (Signoret).*Parlatoria blanchardii* (Targioni).*Phenacaspis inday* (Banks).*Rolaspis chaetachmae* (Brain).*Ptychosperma*.*Andaspis hawaiiensis* (Maskell).

Genera unspecified.

Dentaspis substriata (Newstead).*Diaspis boisduvalii* Signoret.*Fiorinia fioriniae* (Targioni).*Ischnaspis longirostris* (Signoret).*Leucaspis cockerelli* (de Charmoy).*Phenacaspis dilatata* (Green).

PANDANACEAE.

Pandanus.*Pinnaaspis buxi* (Bouché).

PASSIFLORACEAE.

Passiflora.*Pseudaulacaspis pentagona* (Targioni).

PITTOSPORACEAE.

Pittosporum.*Dentachionaspis pittospori* (Hall).

POLYPODIACEAE.

Adiantum.*Pinnaaspis aspidistrae* (Signoret).*Asplenium*.*Pinnaaspis aspidistrae* (Signoret).*Pteris*.*Pinnaaspis aspidistrae* (Signoret).

PROTEACEAE.

Faurea.*Bantudiaspis faureae* Hall.*Ledaspis distincta* (Leonardi).*Leucadendron*.*Rolaspis leucadendri* (Brain).*Protea*.*Asymmetraspis distorta* (Newstead).*Ledaspis distincta* (Leonardi).

Genera unspecified.

Rolaspis lounsburyi (Cooley).

PUNICACEAE.

Punica.*Andaspis punicae* (Laing).

RHAMNACEAE.

Scutia.*Africaspis scutiae* (Brain).*Tecaspis retigera* (Cockerell).*Zizyphus*.*Africaspis communis* (Hall).*Finaspis distincta* (Hall).

ROSACEAE.

Parinarium.*Africaspis parinari* (Hall).*Prunus*.*Pseudaulacaspis pentagona* (Targioni).*Pygaum*.*Inchoaspis pygaei* (Hall).

ROSACEAE continued.

- Pyrus*.
Pseudaulacaspis pentagona (Targioni).
Raphiolepis.
Howardia biclavis (Comstock).
Rosa.
Aulacaspis rosae Bouché.

RUBIACEAE.

- Bouvardia*.
Pseudaulacaspis pentagona (Targioni).
Cinchona.
Africaspis chionaspiformis (Newstead).
Coffea.
Dentachionaspis richiei (Laing).
Diaspis boisduvalii Signoret.
Ischnaspis longirostris (Signoret).
Mitragyne.
Incisaspis pugionifera (Lindinger).

RUTACEAE.

- Calodendron*.
Andaspis hawaiiensis (Maskell).
Phenacaspis dilatata (Green).
Citrus.
Ischnaspis longirostris (Signoret).
Lepidosaphes beckii (Newman).
Lepidosaphes gloverii (Packard).
Parlatoria camelliae Comstock.
Parlatoria pergandii (Comstock).
Parlatoria zizyphi (Lucas).
Pinnaaspis proxima (Leonardi).
Unaspis citri (Comstock).

Diosma.

- Versiculaspis diosmae* (Brain).

Murraya.

- Lepidosaphes beckii* (Newman).

Teclea.

- Dentaspis hargreavesi* (Laing).

SALICACEAE.

- Populus*.
Pseudaulacaspis pentagona (Targioni).

Salix.

- Lepidosaphes beckii* (Newman).
Pudasaspis newsteadii (Leonardi).
Rolaspis munroi sp. n.
Tecaspis kiggelariae (Brain).

SALVADORACEAE.

- Dobera*.
Ledaspis reticulata (Malenotti).

SANTALACEAE.

- Osyris*.
Inchoaspis argentata (Hall).

SAPINDACEAE.

- Allophylus*.
Tecaspis allophylli (Hall).
Tecaspis umtalii (Hall).

SAPOTACEAE.

- Chrysophyllum*.
Howardia biclavis (Comstock).
Mimusops.
Andaspis hawaiiensis (Maskell).
Sideroxylon.
Chionaspis usambarica Lindinger.

SCROPHULARIACEAE.

- Veronica*.
Pseudaulacaspis pentagona (Targioni).

SOLANACEAE.

- Lycium*.
Ambigaspis lycii (Brain).
Solanum.
Andaspis hawaiiensis (Maskell).
Pseudaulacaspis pentagona (Targioni).

STERCULIACEAE.

- Dombeya*.
Hulaspis dombeyae (Hall).
Sterculia.
Chionaspis sterculiae Laing.
Pseudaulacaspis pentagona (Targioni).

THEACEAE.

- Camellia*.
Fiorinia floriniae (Targioni).

ULMACEAE.

- Celtis*.
Fiorinia floriniae (Targioni).
Chaetachme.
Ischnaspis longirostris (Signoret).
Rolaspis carissae (Cockerell).
Rolaspis chaetachmae (Brain).
Tecaspis retigera (Cockerell).

VERBENACEAE.

- Duranta*.
Howardia biclavis (Comstock).

VITACEAE.

- Vitis*.
Pseudaulacaspis pentagona (Targioni).

ZYGOPHYLLACEAE.

- Balanites*.
Ledaspis reticulata (Malenotti).
Ledaspis reticulata var. *minor* (Malenotti).
Tecaspis visci (Brain).

REFERENCES.

- BALACHOWSKY, A., 1928, *Bull. Soc. Hist. nat. Afr. N.* 19.
 —, 1929, *Rev. Path. vég.*
 BANKS, C. S., 1906, *Philipp. J. Sci.* 1.
 BERLESE, A., and LEONARDI, G., 1895, *Riv. Patol. veg.* 3.
 —, —, 1896, *Riv. Patol. veg.* 4.
 BOUCHÉ, P. Fr., 1833, *Schädl. Gart. Ins.*
 —, 1834, *Natursg. Ins.*
 —, 1851, *Stett. ent. Ztg* 12.

- BRAIN, C. K., 1919, *Bull. ent. Res.* 9.
 —, 1920, *Bull. ent. Res.* 10.
 —, 1924, *Ann. Univ. Stellenbosch* 2, Sect. A: 1-44.
 COCKERELL, T. D. A., 1892, *J. Inst. Jam.* 1.
 —, 1893, *Ent. mon. Mag.* 29.
 —, 1897, *Amer. Nat.* 31.
 —, 1898, *Canad. Ent.* 31.
 —, 1898a, *Ann. Mag. nat. Hist.* (7) 1.
 —, 1899, *Canad. Ent.* 31.
 —, 1901, *Entomologist* 34.
 —, 1902, *Entomologist* 35.
 —, 1902a, *Bull. Soc. ent. Fr.* 71.
 —, 1902b, *Ann. Mag. nat. Hist.* (7) 9.
 —, 1906, *Ann. Mag. nat. Hist.* (7) 18.
 COLVÉE, P., 1880, *Gac. Agric. del. Min. de Fomento* 14.
 COMSTOCK, J. H., 1881, *Rep. U.S. Dep. Agric.* 1880.
 —, 1883, *2nd Rep. Dep. Ent. Corn. Univ.*
 COOLEY, R. A., 1898, *Canad. Ent.* 30.
 —, 1899, *Spec. Bull. Mass. Expt. Stn.*
 COOLEY, R. A., and COCKERELL, T. D. A., 1899, *Canad. Ent.* 31.
 COSTA, O. G., 1828, *Prospetto nuova Div. Met. Coccus.*
 —, 1835, *Faun. Reg. Nap. Cocc.*
 CURTIS, W., 1843, *Gard. Chron.*
 DE CHARMOY, E., 1899, *Proc. Soc. Amic. Scien.*
 DOANE, R. W., and FERRIS, G. F., 1919, *Bull. ent. Res.* 6.
 DOUGLAS, J. W., 1887, *Ent. mon. Mag.* 24.
 FERNALD, M. E., 1903, *Cat. Cocc. World.*
 FERRIS, G. F., 1936, *Microentomology* 1.
 —, 1937, *Atlas Scale Insects N. America*, Series I.
 —, 1937a, *Microentomology* 2.
 —, 1938, *Atlas Scale Insects N. America*, Series II.
 —, 1938a, *Microentomology* 3.
 —, 1941, *Atlas Scale Insects N. America*, Series III.
 —, 1941a, *Microentomology* 6.
 —, 1942, *Atlas Scale Insects N. America*, Series IV.
 GHESQUIÈRE, J., 1932, *Bull. Cercl. zool. congol.* 9.
 GOWDEY, C. C., 1913, *Bull. ent. Res.* 4.
 GREEN, E. E., 1896, *Indian Mus. Notes* 4: 1.
 —, 1899, *Cocc. Ceylon* 2.
 —, 1926, *Ent. mon. Mag.* 62.
 GREEN, E. E., and LAING, F., 1923, *Bull. ent. Res.* 14.
 HALL, W. J., 1923, *Min. Agric. Egypt, tech. Bull.* 36.
 —, 1928, *Bull. ent. Res.* 19.
 —, 1929, *Bull. ent. Res.* 20.
 —, 1931, *Trans. ent. Soc. Lond.* 79.
 —, 1935, *Stylops* 4.
 —, 1937, *Trans. R. ent. Soc. Lond.* 86.
 —, 1941, *J. ent. Soc. S. Africa* 4.
 —, 1943, *J. ent. Soc. S. Africa* 6.
 —, 1946, *Trans. R. ent. Soc. Lond.* 97.
 KERNER, J. S. VON, 1778, *Naturg. Coccus bromeliae.*
 KUWANA, S. I., 1926, *Imp. Plant Quar. Service Japan, tech. Bull.* No. 4.
 LAING, F., 1925, *Bull. ent. Res.* 16.
 —, 1928, *Entomologist*.
 —, 1929, *Ann. Mag. nat. Hist.* (10) 4.
 —, 1932, *Rev. Zool. Bot. afr.* 23.

- LAING, F., and COCKERELL, T. D. A., 1929, *Amer. Mus. Novit.*; No. 366.
- LEONARDI, G., 1897, *Riv. Patol. veg.* 6.
- , 1903, *Annali Agric. Roma* 5.
- , 1906, *Redia* 3.
- , 1911, *Boll. Lab. Zool. Portici* 5.
- , 1913, *Boll. Lab. Zool. Portici* 7.
- , 1914, *Boll. Lab. Zool. Portici* 8.
- , 1920, *Mon. Cocc. Ital.*
- LINDINGER, L., 1905, *Insektenbörse* 22.
- , 1909, *Jb. hamburg. wiss. Anst.* 26, 3 Beiheft.
- , 1910, *Jb. hamburg. wiss. Anst.* 27, 3 Beiheft.
- , 1912, *Die Schildläuse.*
- , 1913, *Jb. hamburg. wiss. Anst.* 30, 3 Beiheft.
- , 1931, *Ent. Rdsch.* 48.
- , 1932, *Wien. ent. Ztg* 49.
- , 1932a, *Ent. Rdsch.* 49.
- , 1932b, *Konowia* 11.
- , 1934, *Ent. Jb.*
- , 1934a, *Ent. Anz.* 14.
- , 1935, *Ent. Jb.*
- , 1936, *Ent. Jb.*
- , 1937, *Ent. Jb.*
- LUCAS, H., 1853, *Bull. Soc. ent. Fr.* (3) 1.
- MACGILLIVRAY, A. D., 1921, *The Coccidae.*
- MALENOTTI, E., 1916, *Redia* 11.
- MARCHAL, P., 1909, *Mem. Soc. zool. Fr.*
- MASKELL, W. M., 1879, *Trans. N.Z. Inst.* 12.
- , 1884, *Trans. N.Z. Inst.* 17.
- , 1894, *Trans. N.Z. Inst.* 27.
- , 1896, *Trans. N.Z. Inst.* 28.
- , 1897, *Trans. N.Z. Inst.* 29.
- McKENZIE, H. L., 1945, *Microentomology* 10.
- MORGAN, A. C. F., 1890, *Ent. mon. Mag.* 26.
- MORRISON, H., 1939, *U.S. Dep. Agric. Misc. Pub.* 344.
- MORRISON, H. and E., 1922, *Proc. U.S. nat. Mus.* 60, Art. 12.
- MUNRO, H. K., and FOUCHÉ, F. A., 1936, A list of the Scale Insects and Mealy Bugs and their Host Plants in South Africa. *Dept. Agric. Bull.* No. 158.
- NEWMAN, E., 1869, *Entomologist* 4.
- NEWSTEAD, R., 1898, *Ent. mon. Mag.* 34.
- , 1901, *Ent. mon. Mag.* 37.
- , 1901a, *Mon. Brit. Cocc.* 1.
- , 1906, *Liverpool Univ. quart. J.* 1, 2.
- , 1908, *J. econ. Biol.* 3.
- , 1910, *Bull. ent. Res.* 1.
- , 1911, *Bull. ent. Res.* 2.
- , 1911a, *Mitt. zool. Mus. Berl.* 5.
- , 1912, *Zool. anthr. Ergeb. westl. zentr. Sudaf.* 5.
- , 1913, *Bull. ent. Res.* 4.
- , 1914, *Bull. ent. Res.* 4.
- , 1917, *Bull. ent. Res.* 7.
- , 1917a, *Bull. ent. Res.* 8.
- , 1920, *Bull. ent. Res.* 10.
- PACKARD, A. S., 1869, *Guide to Study of Ins.* Ed. 1.
- SANDERS, J. G., Supplements 1 and 2 to Fernald's *Cat. Cocc. World.*
- , 1906, *U.S. Dept. Agric., tech. Ser.* 12, 1.
- , 1909, *U.S. Dept. Agric., tech. Ser.* 16, 3.

- SASSCER, E. R., Supplements 3-6 to Fernald's *Cat. Cocc. World*.
—, 1911, *U.S. Dept. Agric., tech. Ser.* **16**, 4 : 61-74.
—, 1912, *U.S. Dept. Agric., tech. Ser.* **16**, 6 : 83-97.
—, 1913, *U.S. Dept. Agric., tech. Ser.* **16**, 7 : 99-116.
—, 1915, *Proc. ent. Soc. Wash.* **17** (1) : 25-38.
SCHRANK, Fr. de P., 1781, *Enum. Ins. Austr.*
SEABRA and VAYSSIÈRE, P., 1918, *Bull. Soc. ent. Fr.*
SHIMER, H., 1868, *Trans. Amer. ent. Soc.* **1**.
SIGNORET, V., 1869, *Ann. Soc. ent. Fr.* **9**.
—, 1882, *Bull. Soc. ent. Fr.* (6) **2**.
SULC, K., 1895, *S.B. böhm. Ges. Wiss.* **49**.
TAKAHASHI, R., 1931, *Trans. nat. hist. Soc. Formosa* **21**.
TARGIONI, T., 1867, *Stud. sul. Cocc.*
—, 1869, *Catalogue*.
—, 1885, *Rev. di Bacch.*, No. **11**.
VAYSSIÈRE, P., 1912, *Bull. Soc. ent. Fr.*
—, 1913, *Rev. Phytopath. appl.* **1** : 9.
—, 1914, *Bull. Soc. ent. Fr.*
ZEHTNER, L., 1898, *Mede Proef Suik Java* **3**.

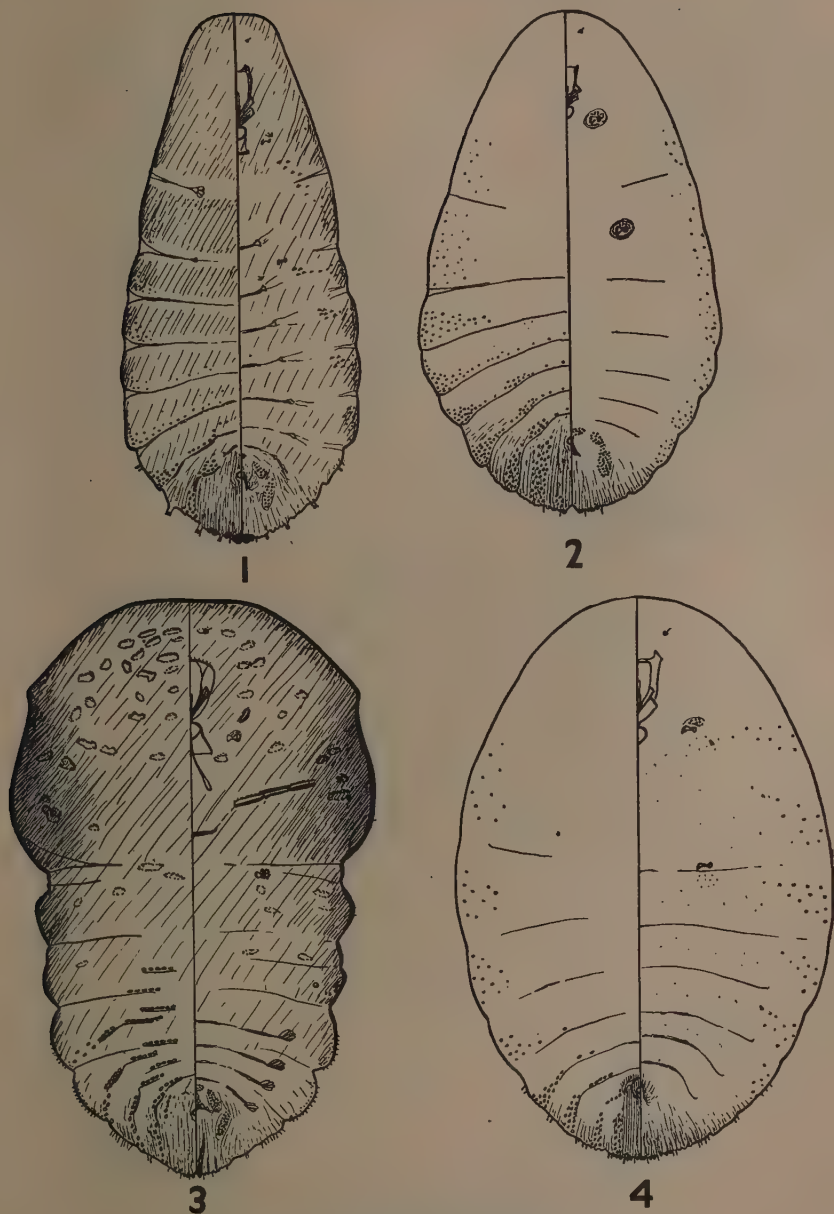
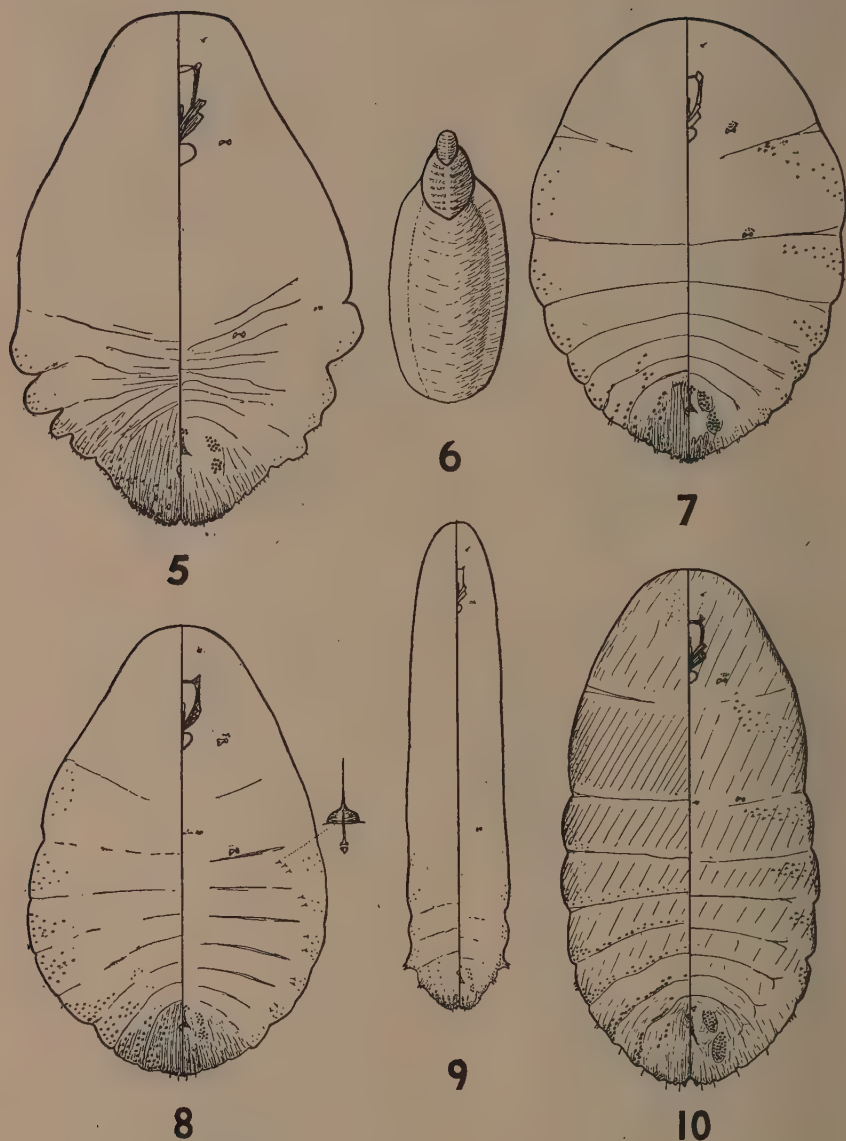


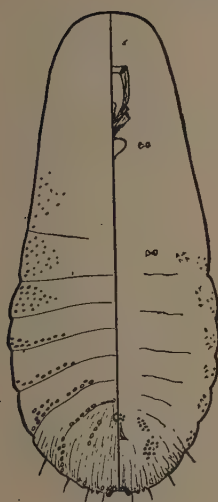
FIG. 1.—*Africaspis caffra* (Brain).

FIG. 2.—*Augulaspis nudata* (Newstead)—genotype.

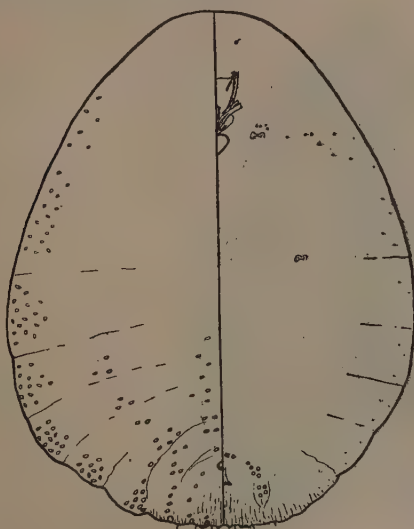
FIG. 3.—*Aulacaspis fulleri* (Cockerell).

FIG. 4.—*Balaspis faurei* gen. and sp. n.—genotype.

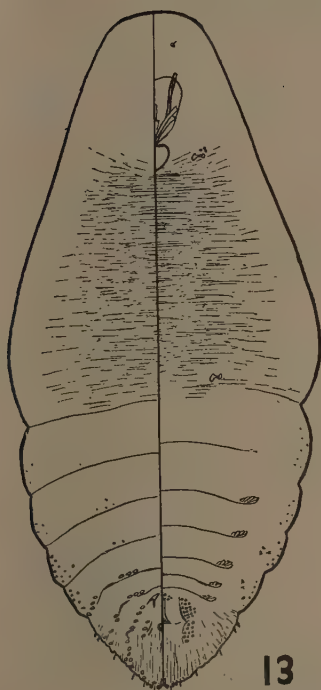
FIG. 5.—*Chionaspis* "lutea" Newstead.FIG. 6.—*Chionaspis* "lutea" Newstead—scale of adult ♀.FIG. 7.—*Contigaspis naudei* sp. n.FIG. 8.—*Contigaspis subnudata* (Newstead)—genotype.FIG. 9.—*Daraspis bussii* (Newstead)—genotype.FIG. 10.—*Dentachionaspis margaritae* (Brain).



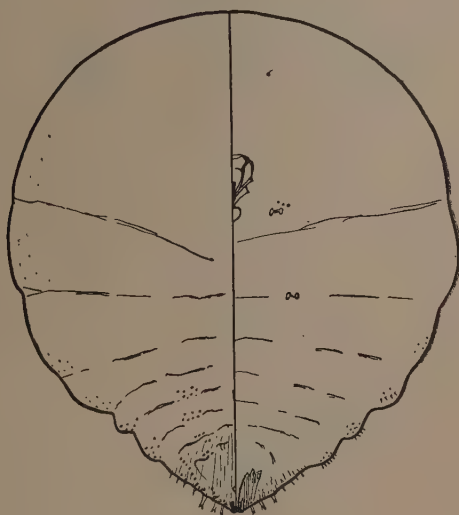
11



12



13



14

FIG. 11.—*Dentachionaspis pseudonivea* (Malenotti).

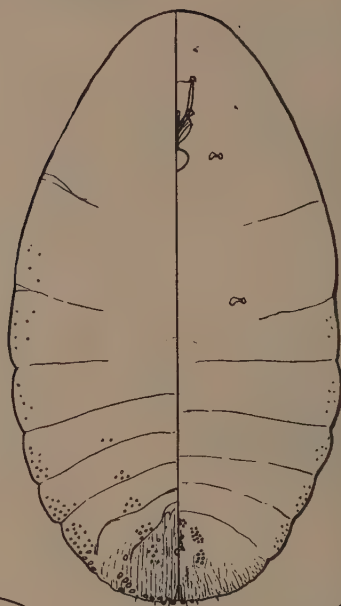
FIG. 12.—*Dentaspis globosus* (Brain).

FIG. 13.—*Duplachionaspis stanotophri* (Cooley).

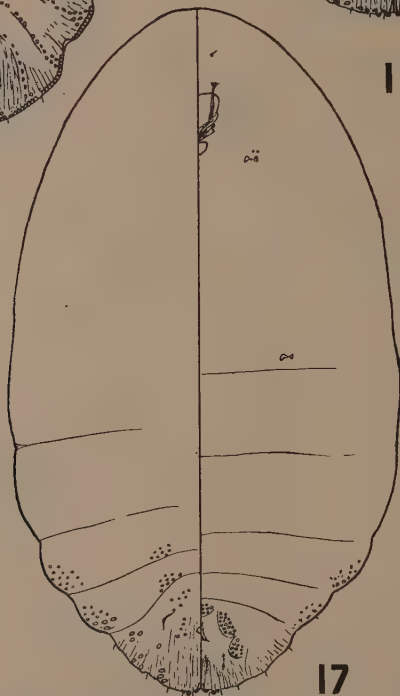
FIG. 14.—*Hulaspis dombeyae* (Hall)—genotype.



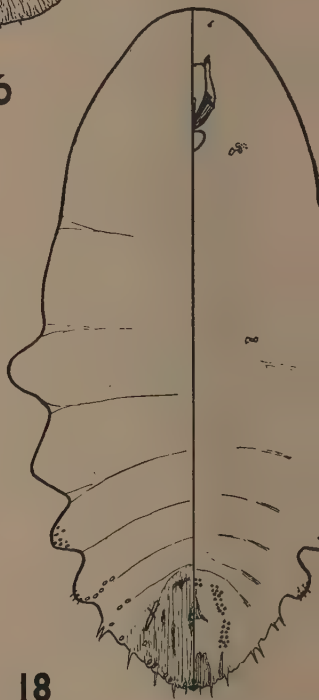
15



16



17



18

FIG. 15.—*Moraspis euphorbiae* (Brain)—genotype.
FIG. 16.—*Nelaspis exalbida* (Cockerell)—genotype.

FIG. 17.—*Nelaspis humilis* (Brain).
FIG. 18.—*Pinnaaspis gossypii* (Newstead).

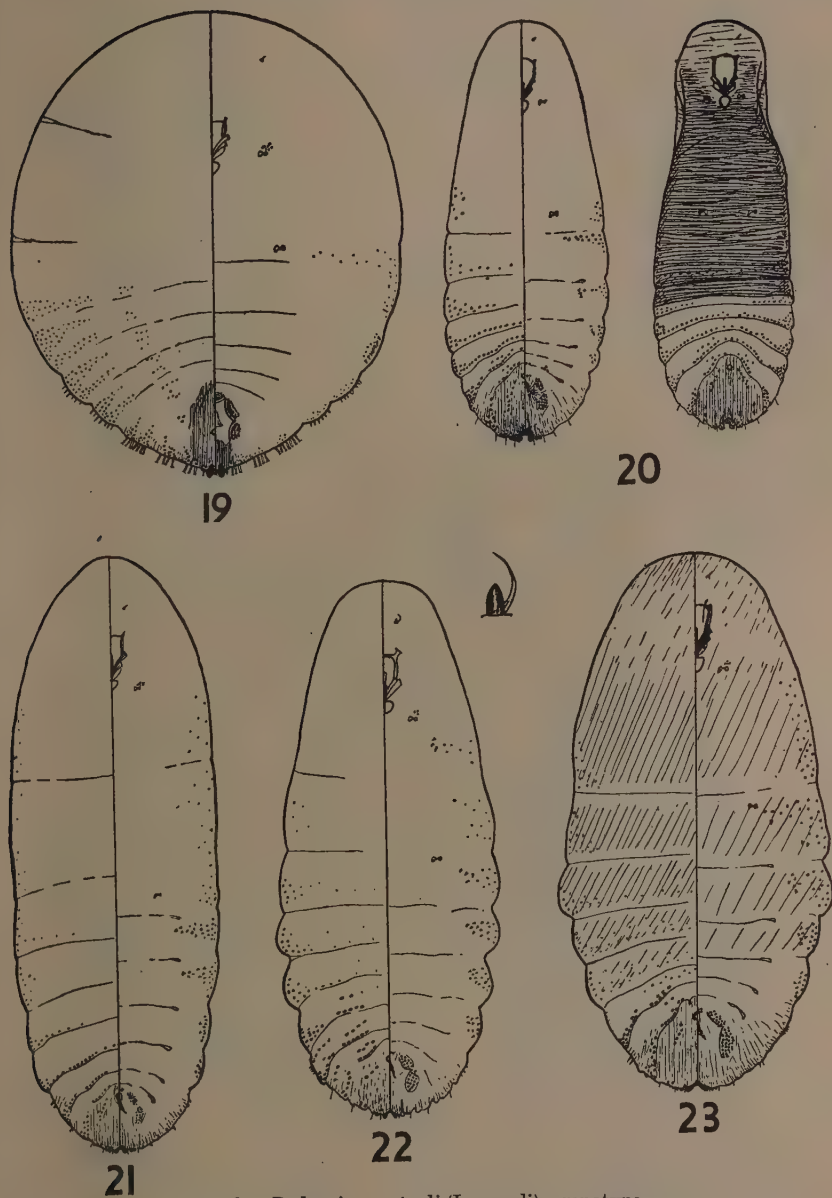


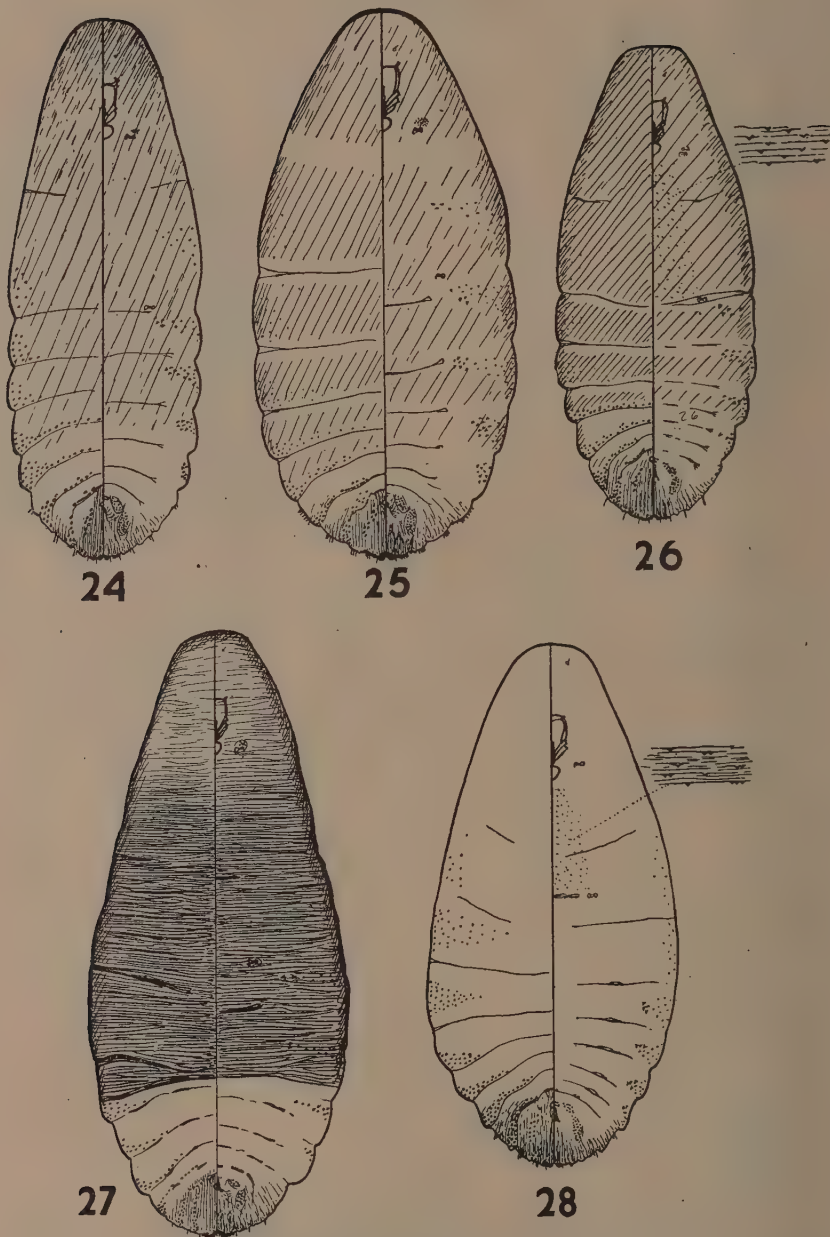
FIG. 19.—*Pudaspsis newsteadi* (Leonardi)—genotype.

FIG. 20.—*Rolaspis carissae* (Cockerell)—early adult ♀ on left, mature adult ♀ on right.

FIG. 21.—*Rolaspis chaetachmae* (Brain).

FIG. 22.—*Rolaspis compositae* sp. n.

FIG. 23.—*Rolaspis leucadendri* (Brain).

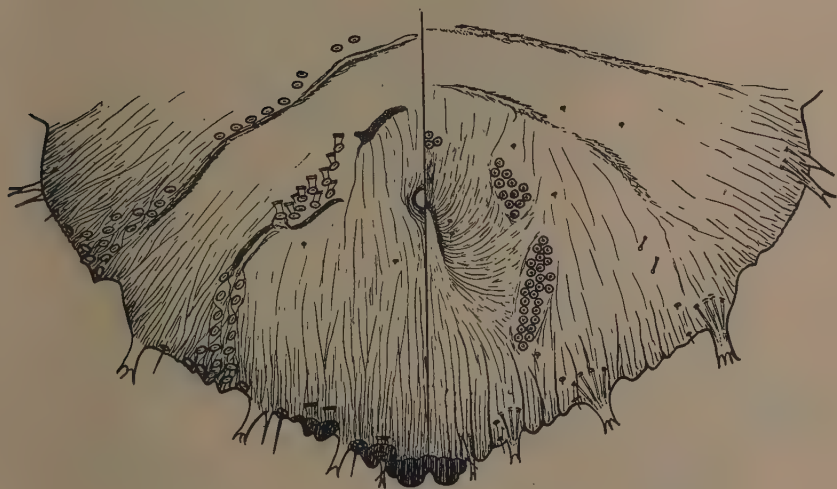
FIG. 24.—*Rolaspis lounsburyi* var. *ekebergiae* (Brain).FIG. 25.—*Rolaspis munroi* sp. n.FIG. 26.—*Rolaspis spiculata* new name for *Chionaspis chaetachmae* var. *imbricata* Hall.FIG. 27.—*Tecaspis kiggelariae* (Brain).FIG. 28.—*Tecaspis mytilaspiformis* (Newstead).



29



30



31

FIG. 29.—*Tecaspis visci* (Brain).

FIG. 30.—*Voraspis nigerensis* (Vayssi re).

FIG. 31.—*Africaspis caffra* (Brain).

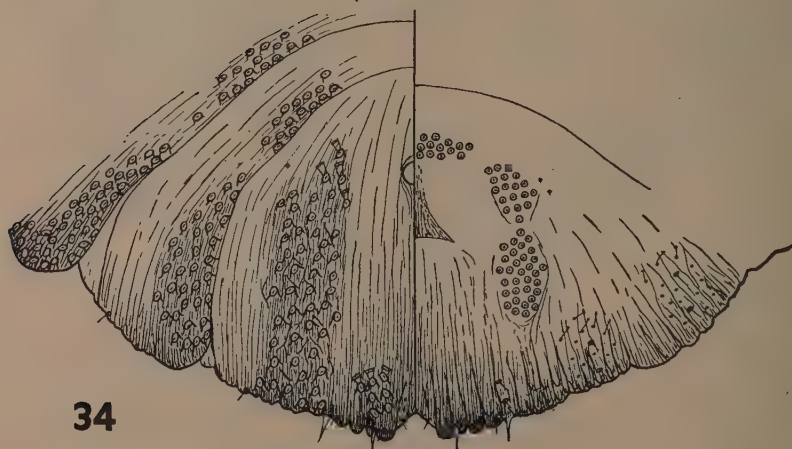
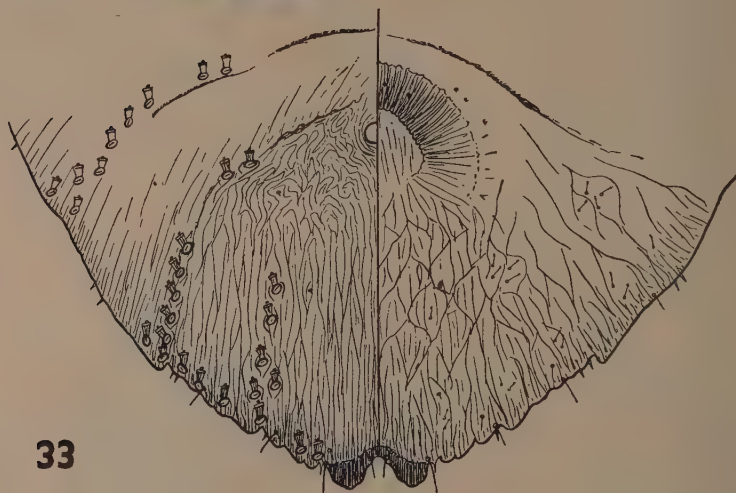
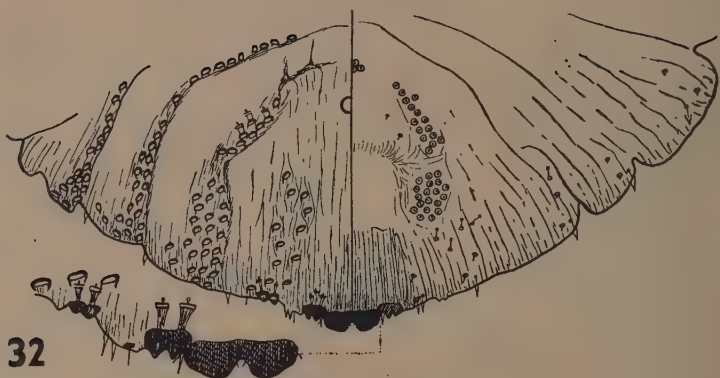
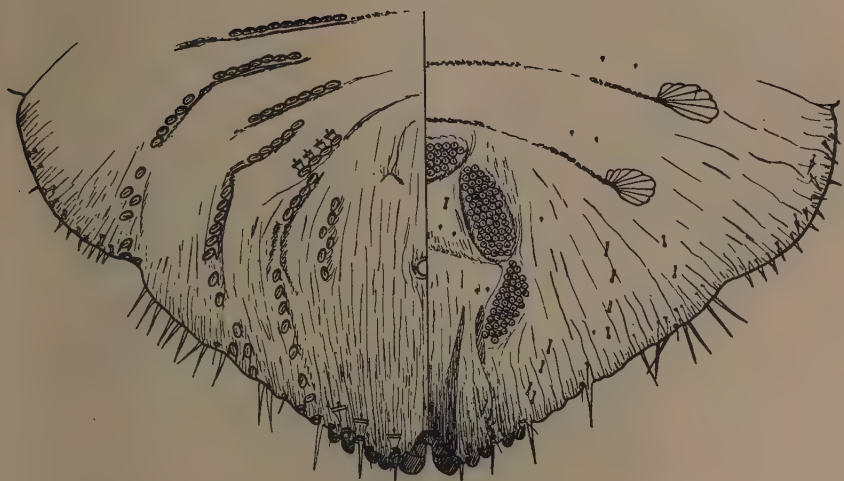
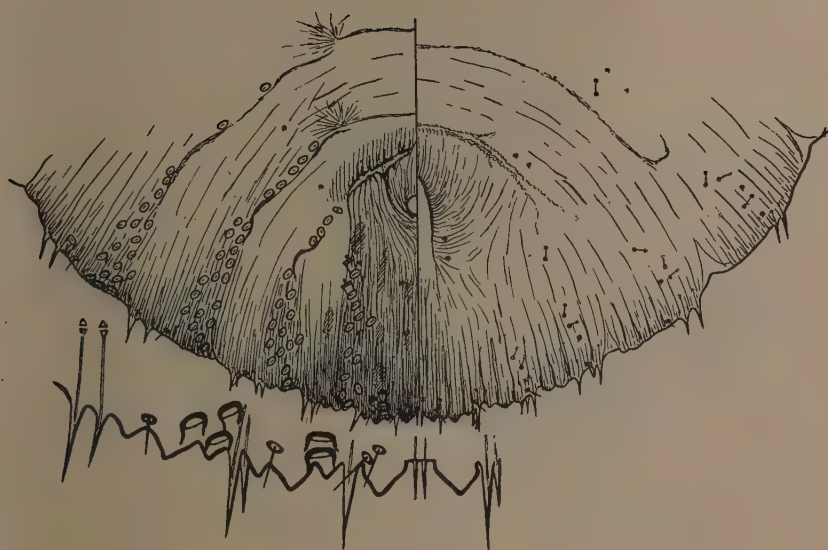


FIG. 32.—*Africaspis scutiae* (Brain).
 FIG. 33.—*Asymmetrasis distorta* (Newstead)—genotype.
 FIG. 34.—*Augulaspis nudata* (Newstead)—genotype.



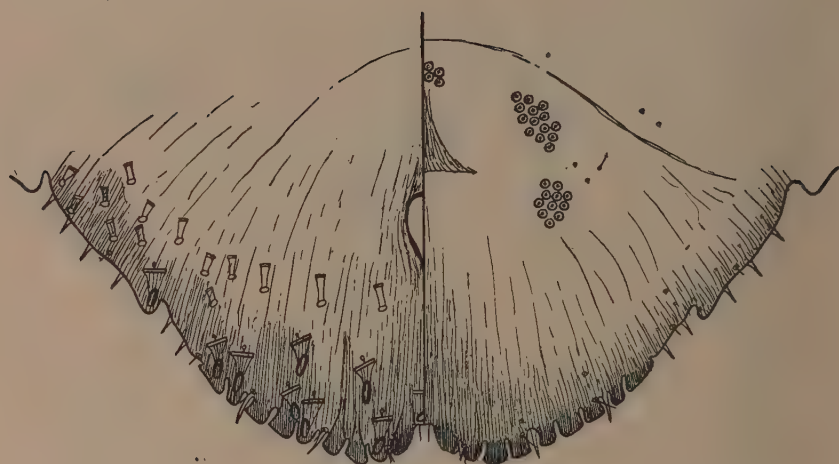
35



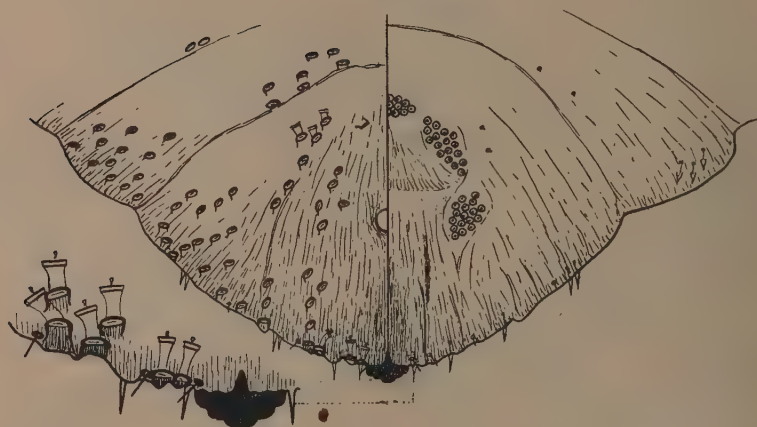
36

FIG. 35.—*Aulacaspis fulleri* (Cockerell).

FIG. 36.—*Balaspis faurei* gen. and sp. n.—genotype.

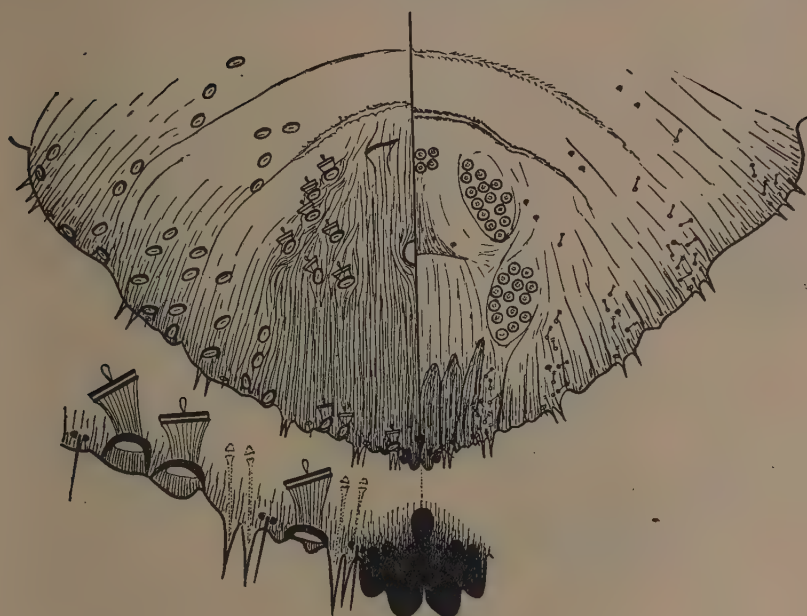


37

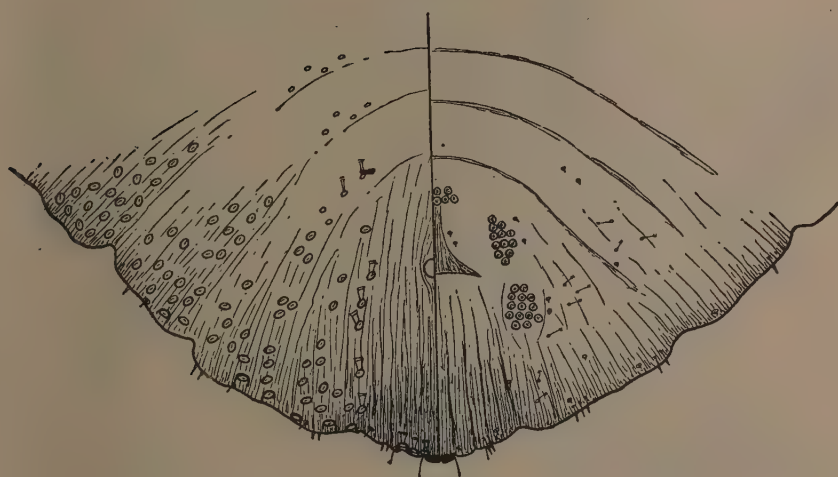


38

FIG. 37.—*Chionaspis* "lutea" Newstead.FIG. 38.—*Contigaspis cyanogena* (Brain).



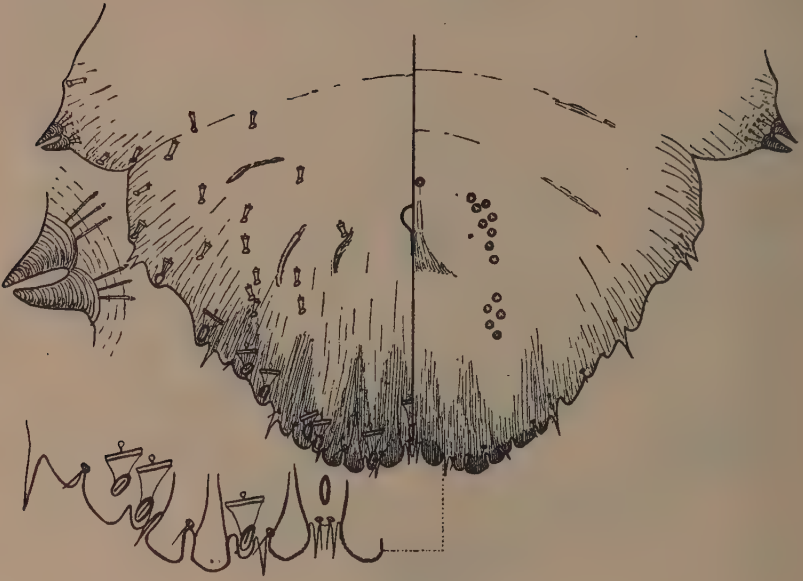
39



40

FIG. 39.—*Contigaspis naudei* sp. n.

FIG. 40.—*Contigaspis subnudata* (Newstead)—genotype.



41



42

FIG. 41.—*Daraspis bussii* (Newstead)—genotype.
FIG. 42.—*Dentachionaspis margaritae* (Brain).

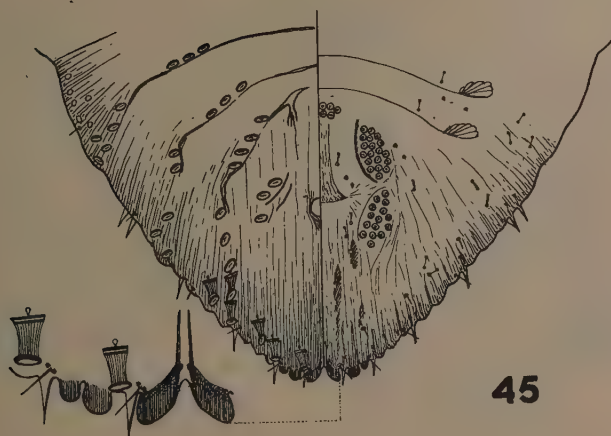
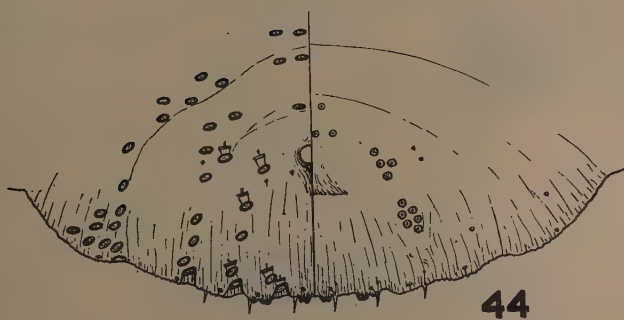
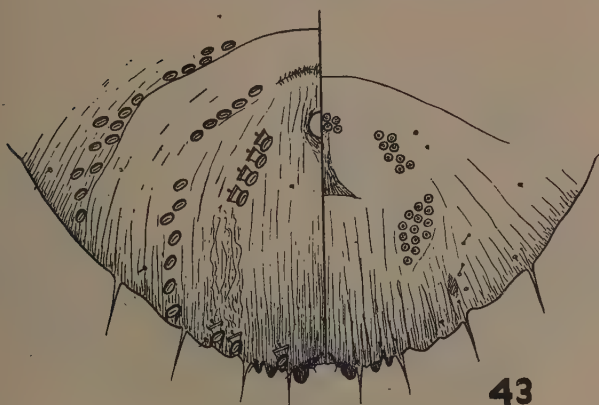


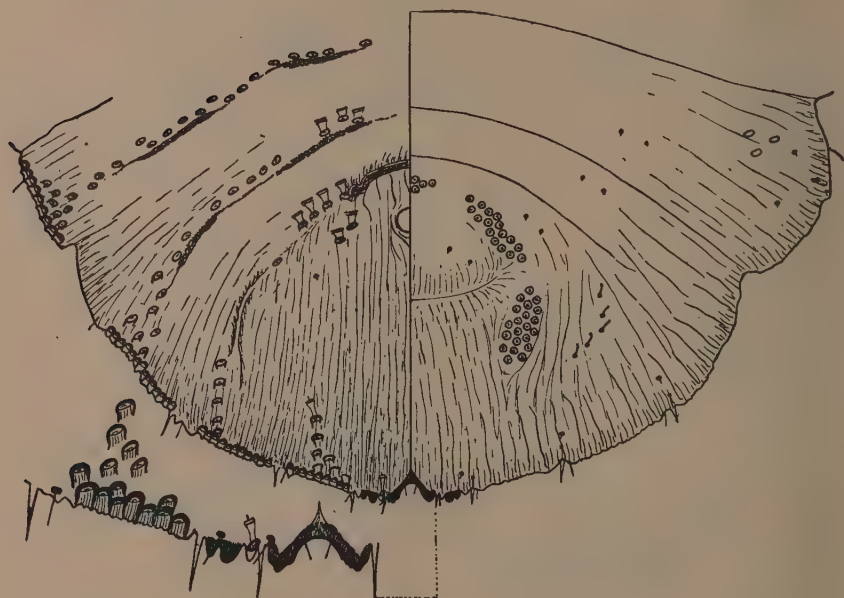
FIG. 43.—*Dentachionaspis pseudonivea* (Malenotti).

FIG. 44.—*Dentaspis globosus* (Brain).

FIG. 45.—*Duplachionaspis stanotophri* (Cooley).



46



47

FIG. 46.—*Hulaspis dombeyae* (Hall)—genotype.
FIG. 47.—*Moraspis euphorbiae* (Brain)—genotype.

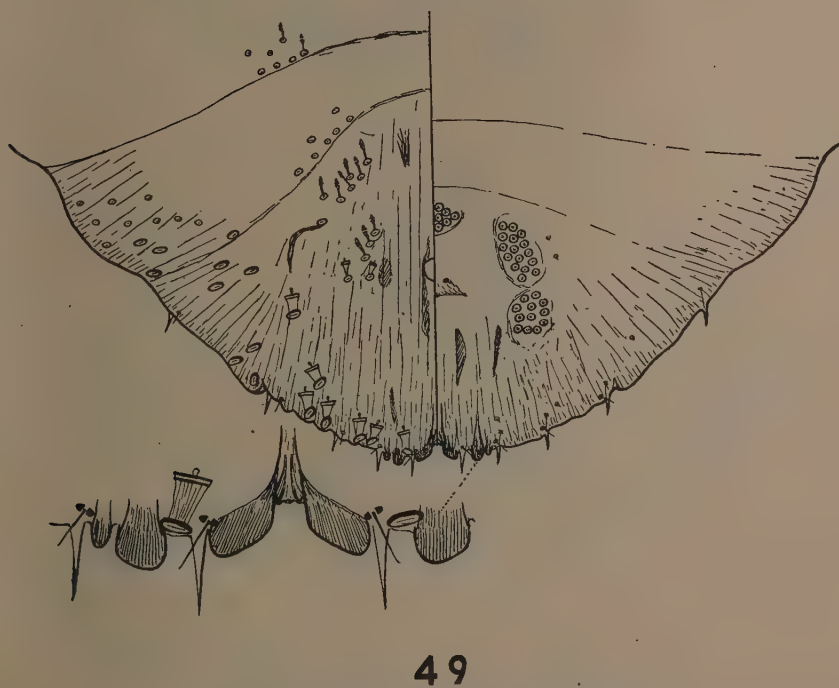
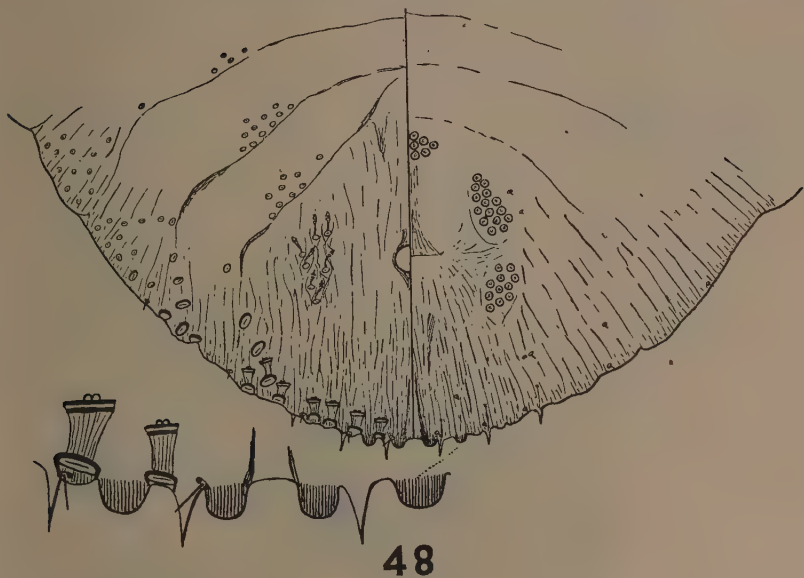
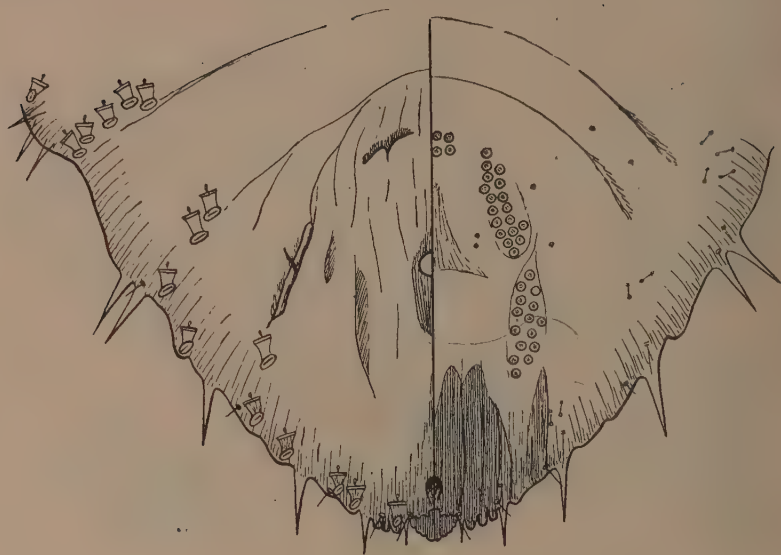
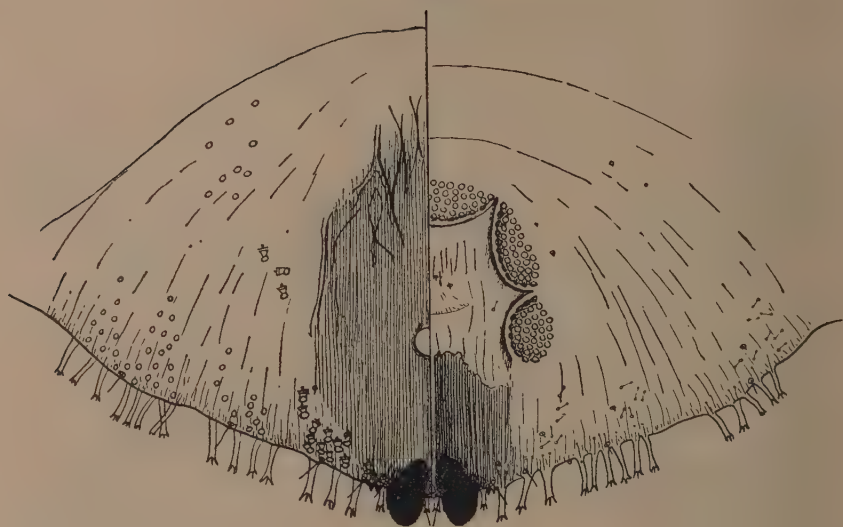


FIG. 48.—*Nelaspis exalbida* (Cockerell)—genotype.
FIG. 49.—*Nelaspis humilis* (Brain).



50

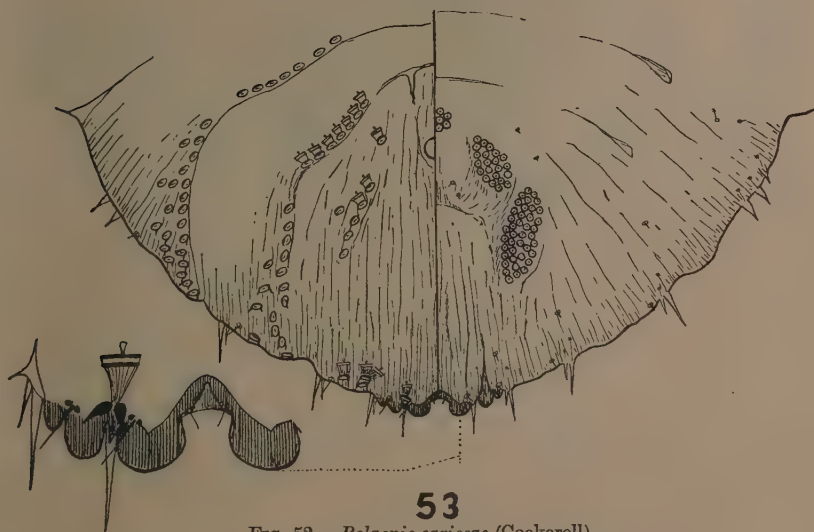


51

FIG. 50.—*Pinnaspis gossypii* (Newstead).FIG. 51.—*Pudaspis newsteadii* (Leonardi)—genotype.



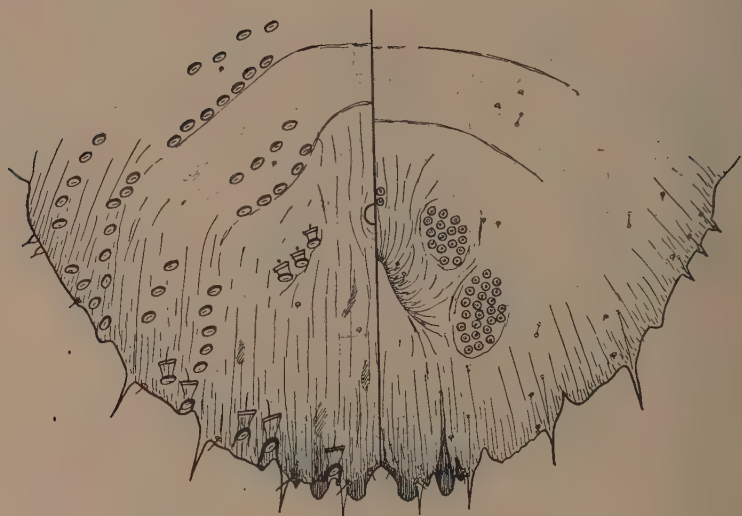
52



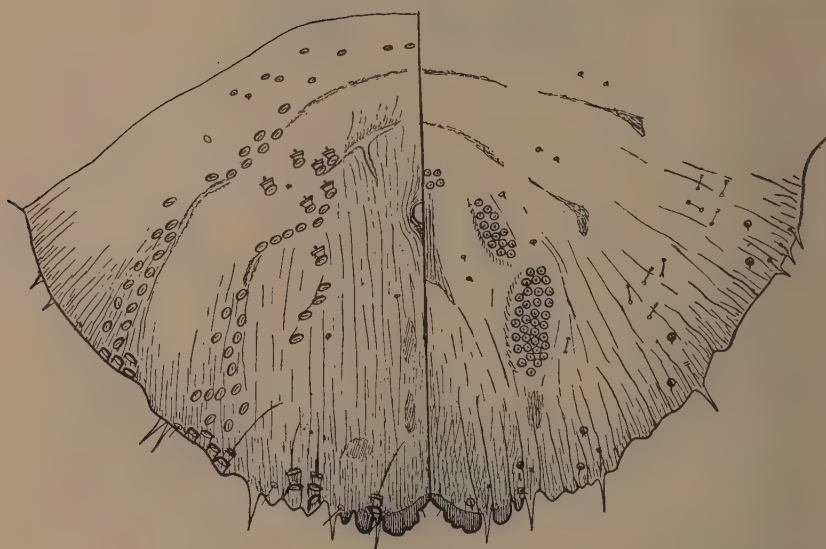
53

FIG. 52.—*Rolaspis carissae* (Cockerell).

FIG. 53.—*Rolaspis chaetachmae* (Brain).

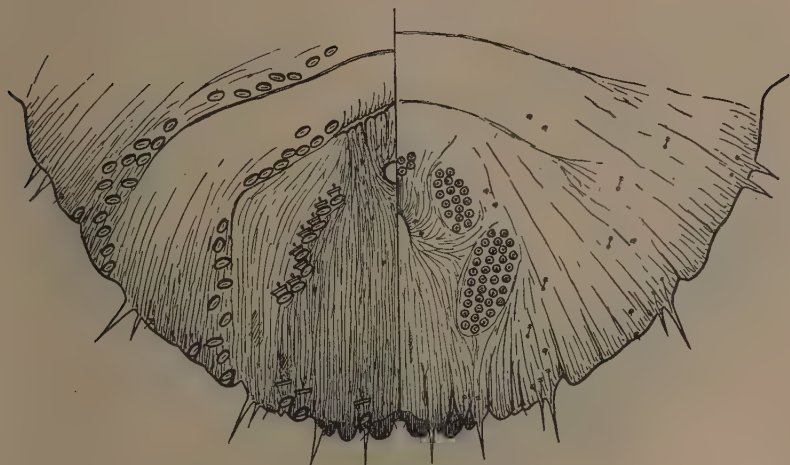


54

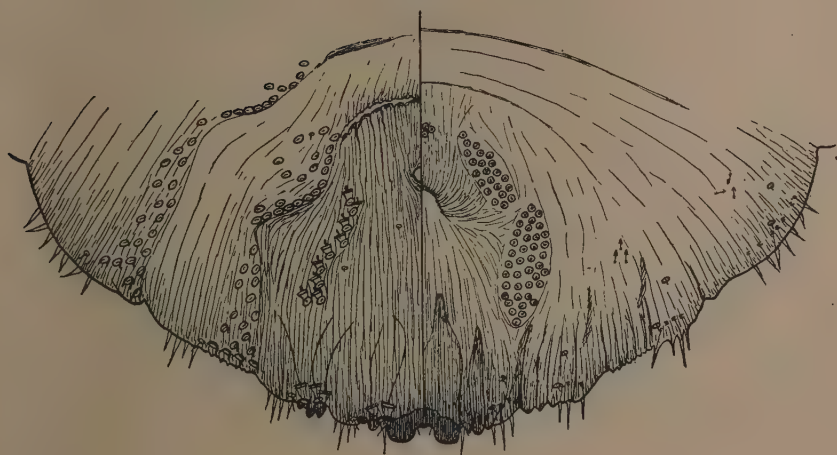


55

FIG. 54.—*Rolaspis compositae* sp. n.
FIG. 55.—*Rolaspis leucadendri* (Brain).



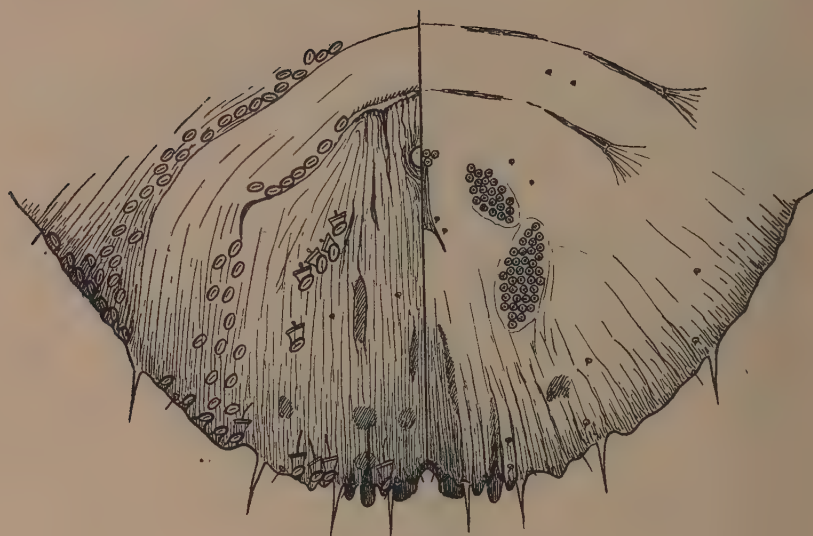
56



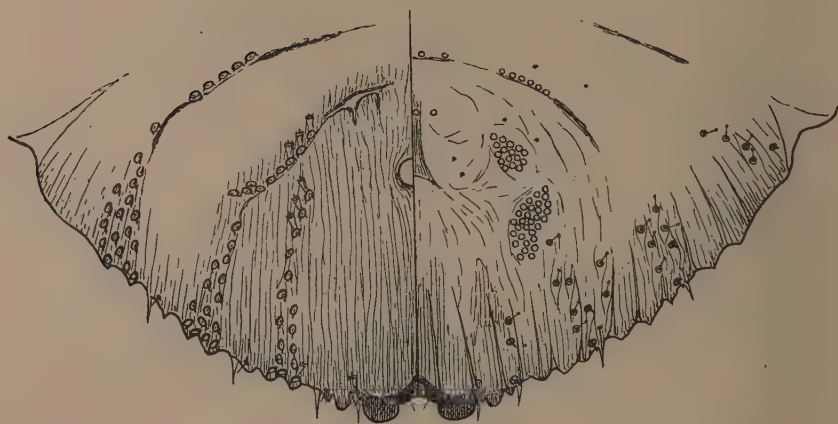
57

FIG. 56.—*Rolaspis lounsburyi* var. *ekebergiae* (Brain).

FIG. 57.—*Rolaspis munroi* sp. n.



58



59

FIG. 58.—*Rolaspis spiculata*, new name for *Chionaspis chaetachmae* var. *imbricata* Hall.
FIG. 59.—*Tecaspis kiggelariae* (Brain).

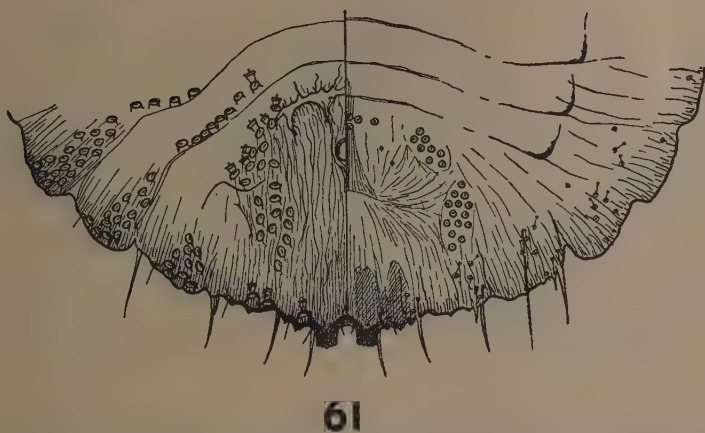
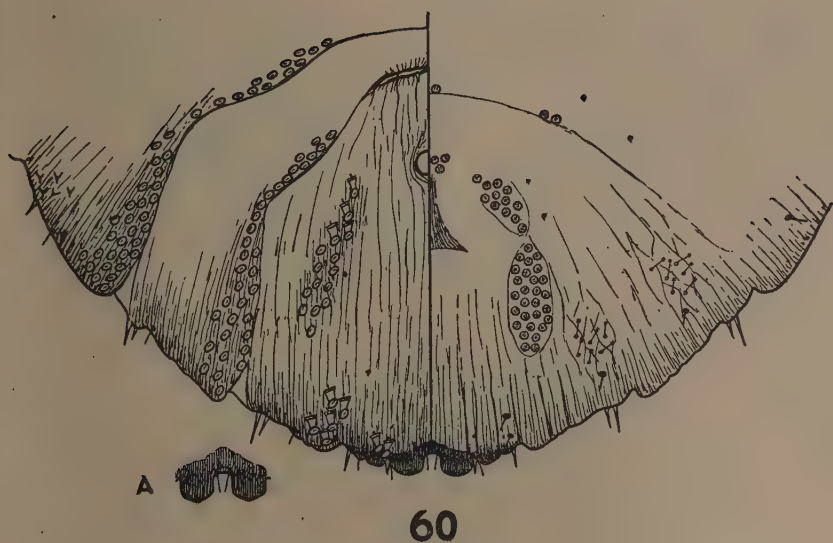


FIG. 60.—*Tectaspis mytilaspiformis* (Newstead); A, variation in shape of median lobes.
FIG. 61.—*Tectaspis retigera* (Cockerell).

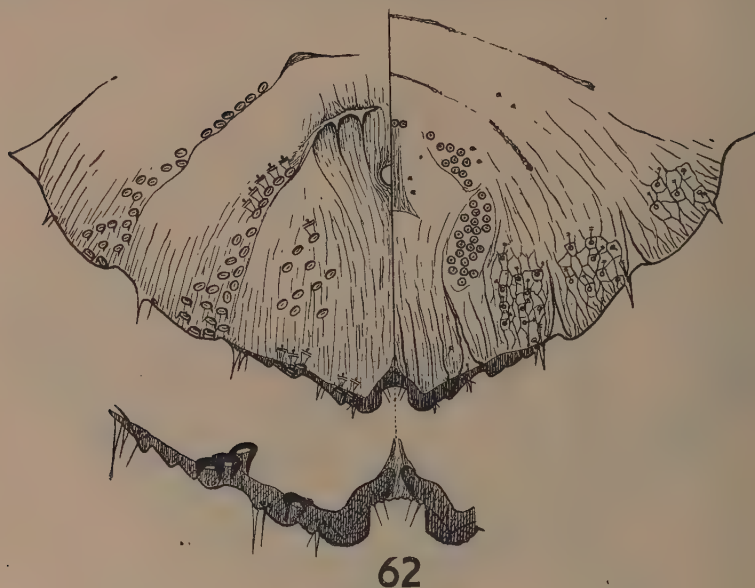
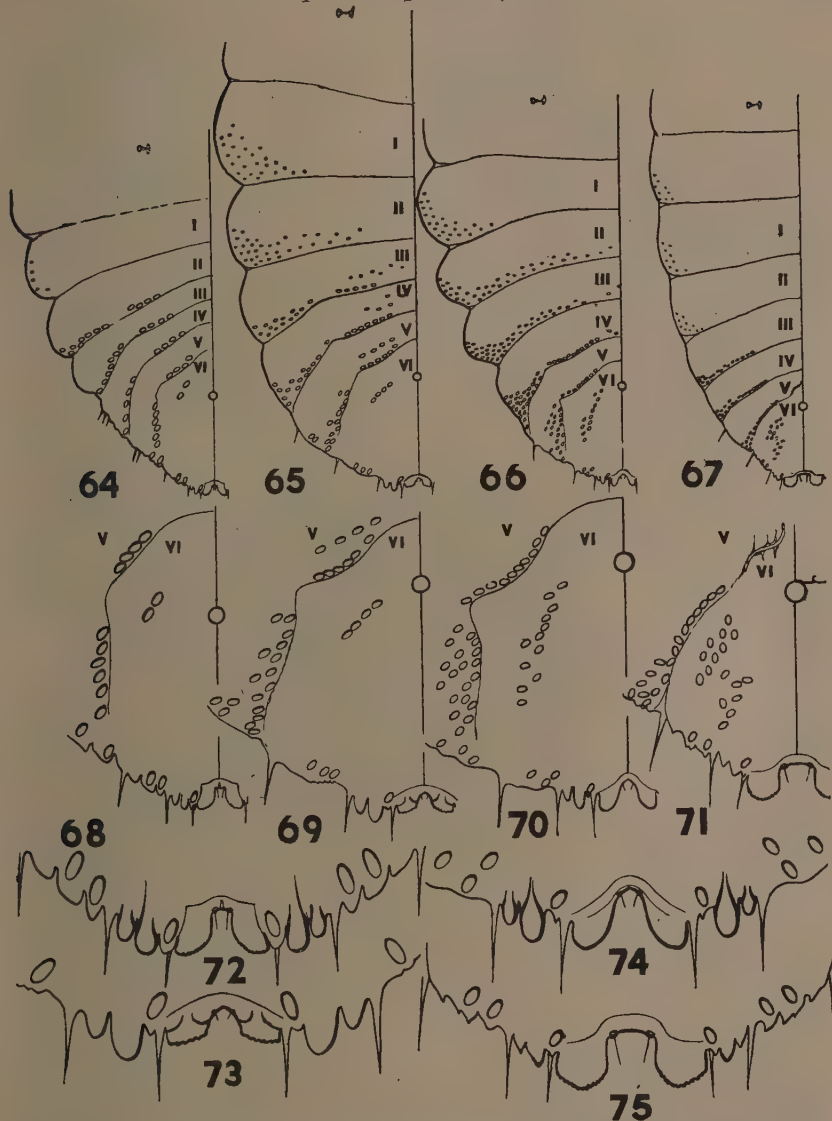


FIG. 62.—*Tecaspis visci* (Brain).
 FIG. 63.—*Voraspis nigerensis* (Vayssière).

Characters distinguishing the genera *Phenacaspis*, *Voraspis*, *Rolaspis* and *Tecaspis*.
 Dorsal aspect of pygidium and prepygidial segments.

- FIG. 64.—*Phenacaspis dilatata* (Green).
 FIG. 65.—*Voraspis carpenteri* (Laing).
 FIG. 66.—*Rolaspis whitehilli* (Hall).
 FIG. 67.—*Tecaspis umtalii* (Hall).



Dorsal aspect of pygidium showing the arrangement of dorsal pores on segments 5 and 6.

FIG. 68.—*Phenacaspis dilatata* (Green).

FIG. 69.—*Voraspis carpenteri* (Laing).

FIG. 70.—*Rolaspis whitehilli* (Hall).

FIG. 71.—*Tecaspis umtalii* (Hall).

Median portion of pygidial fringe showing the median and second lobes.

FIG. 72.—*Phenacaspis dilatata* (Green).

FIG. 73.—*Voraspis carpenteri* (Laing).

FIG. 74.—*Rolaspis whitehilli* (Hall).

FIG. 75.—*Tecaspis umtalii* (Hall).

The lengths of the actual specimens—all types—figured were as follows:—*Phenacaspis dilatata* (Green), 0.9 mm.; *Voraspis carpenteri* (Laing), 1.85 mm.; *Rolaspis whitehilli* (Hall), 2.2 mm.; *Tecaspis umtalii* (Hall), 1.75 mm.

GENERAL INDEX

A

- Aceratagallia*, 160.
Acherontia atropos, 432.
Acidia heraclei, 362.
 ACONTINAE, 237.
 ACRONICTINAE, 237.
acutaeangulata, *Anacertagallia laevis*, 159.
 ADELIDAE, 2.
adnexa, *Coryphaeschna*, 467.
Adoretus, 495.
Adoretus punctipennis, 495.
Adoretus versutus, 495.
adulatrix, *Eusemia*, 251.
Aeloagrion flammeum, 458.
aequalis, *Micathyria*, 221.
Aeschnosoma, 472.
 AESHNIDAE, 466.
Aetalion, 39.
 AETALIONIDAE, 39.
Aetalion reticulatum, 41.
 AETHALIONIDAE, 39.
Agapetus, 196.
Agapetus fuscipes, 198.
 AGARISTINAE, 237.
Agraylea, 196.
Agriogomphus sylvicola, 467, 471.
Agriion extranea, 457.
Agriion extraneum, 457.
 AGROTIDAE, 8, 17.
Agrotis c-nigrum, 238, 242.
Agrotis ypsilon, 247.
Aiteta apriformis, 249.
Aiteta truncata, 249.
Alabama argillacea, 339.
albicans, *Xorides*, 437.
Aleochara bilineata, 356.
 ALEYROIDIDAE, 402.
Allothrombium fuliginosum, 493.
alni, *Apatele*, 24.
Alphitobius, 490.
americana, *Hetaerina*, 225.
americana, *Zenithoptera*, 468.
Ametalla spinolae, 103.
Ametalla stenodera, 103.
Ametalloides gen.n., 102.
Ametalloides punctatus sp.n., 103.
 AMPHIPHYRIDAE, 460, 463.
 AMPHIPHYRINAE, 237.
amphix, *Lyncestia*, 243.
Anacertagallia gen.n., 159.
Anacertagallia laevis acutaeangulata subsp.n., 159.
anatolica, *Hardya*, 168.
Anatolida, 152.
Anchytarsus bicolor, 485.
Androlymnia, 238.
Angitia chrysosticta, 276.
anglicus, *Polydaspis sulcicollis*, 121.
angorensis, *Stenometopiellus*, 176.
angularis, *Oscinella*, 141.
Anomisma terminatum, 463, 464.
 ANOMOSETIDAE, 14.
antennata, *Tropidoscinius*, 136.
Anthracias, 490.
 ANTHRENINAE, 477, 478, 479, 480, 482, 483, 484, 485.
Anthrenocerus, 480, 482.
Anthrenocerus australis, 485.
Anthrenus, 480, 482, 483.
Anthrenus coloratus, 485.
Anthrenus fuscus, 485.
Anthrenus museorum, 485.
Anthrenus verbasci, 485.
Anthrenus vorax, 482, 485.
Aonidiella atomaria sp.n., 55.
Aonidiella chrysobalani, 61.
Aonidiella inopinata, 62.
Aonidiella monotes, 62.
Apatele, 23.
Apatele alni, 24.
Aphanotrigrionum brunneum sp.n., 126.
Aphanotrigrionum fasciella, 127.
Aphanotrigrionum femorella sp.n., 126.
Aphanotrigrionum griseum sp.n., 126.
Aphanotrigrionum griseum var. *curtipenne* var.n., 126.
Aphanotrigrionum inerme sp.n., 128.
Aphanotrigrionum meijerei, 126.
Aphanotrigrionum trilineatum, 125.
 APHIDIDAE, 405.
araxis, *Stenometopiellus*, 176.
Arboridia subgen.n., 153.
 ARCTIDAE, 17.
arenicola, *Chlorita*, 151.
Argia, 443, 444, 445, 449, 453, 456.
Argia cuprea, 445, 447.
Argia dagnina, 453.
Argia difficilis, 220, 228.
Argia extranea euphorbia subsp.n., 457.
Argia extranea extranea, 456.
Argia extranea forficula subsp.n., 456.
Argia frequentula, 453.
Argia garmeri, 453.
Argia hamulata sp.n., 447.
Argia huallaga sp.n., 450.
Argia infrequentula, 451.
Argia kokama, 456.
Argia makoka sp.n., 455.
Argia mishuyaca sp.n., 453, 454, 455, 456.
Argia mollusca sp.n., 454.
Argia orichalcea, 220.
Argia pulla, 453.
Argia translata, 220, 226.
Argia trifoliata sp.n., 449.
Argia umbricaca sp.n., 451.
Argia variegata, 451.
Argynnis, 25.
Argynnis selene, 28.
armigera, *Heliothis*, 24.
Aromia moschata, 429, 432, 437.
 ASEMINAE, 422.
Asianidia subgen.n., 153.
asper, *Polyoptilus*, 98.
Aspidiotus ceardi, 62.
Atalasis sagroides, 104.

ater, *Dermestes*, 484.
atomaria, *Aonidiella*, 55.
atropos, *Acherontia*, 432.
 ATTAGENINAE, 477, 479, 480, 482.
Attagenus, 479, 480, 484.
Attagenus gloriosae, 484.
Attagenus pelloi, 485.
Attagenus piceus, 484.
Attagenus schäfferi, 485.
attenuata, *Erythrodiplox*, 470.
Aulacogaster rufitarsus, 362.
Aulacoscelis candezei, 90.
Aulacoscelis elongata, 88.
Aulacoscelis femorata, 88.
Aulacoscelis fulvipes, 90.
Aulacoscelis grandis, 88.
Aulacoscelis hogei, 90.
Aulacoscelis, key to species, 85.
Aulacoscelis melanocera, 90.
Aulacoscelis melioides sp.n., 89.
Aulacoscelis, notes on genera, 83.
Aulacoscelis purpurea, 90.
Aulacoscelis sanguinea, 89.
Aulacoscelis, systematic position, 78.
Aulacoscelis tibialis, 88.
Aulacoscelis variabilis, 90.
aurantiacum, *Heteragrion*, 466.
auricularius, *Gynacantha*, 467.
auriculatus, *Dryops*, 486.
australis, *Anthrenocerus*, 485.
Austroprosbole maculata, 46.
azerbeidzhanica, *Chlorita uvaroviana*, 151.

B

Balala membracioides, 46.
balia, *Goniopsis* (*Lasiambia*), 123.
barbipes, *Megarhinus*, 177, 179.
basalis, *Erythrodiplox basalis*, 470.
batesi, *Neocordulia*, 472.
bauhiniae, *Phenacaspis*, 65.
bembeciformis, *Sphecia*, 25.
 BIBIONIDAE, 394.
bicolor, *Anchytarsus*, 485.
bicolorana, *Pseudoips*, 475.
bifasciatum, *Rhagium*, 437.
bimaculata, *Thaumaglossa*, 482, 485.
biolleyi, *Orthemis*, 467.
Bledius, 386.
boleti, *Scardia*, 21.
 BOMBYCIDAE, 24.
Borolia byssina, 240.
Botanobia dubia, 134.
Botanobia fascipes, 134.
brassicae, *Pieris*, 29.
brevipalpis, *Megarhinus*, 178.
brunneum, *Aphanotrigonum*, 126.
byssina, *Borolia*, 240.
byzantina, *Hardya* (*Eohardya*), 173.

C

Calamoncosis aprica, 120.
Calamoncosis duinenensis, 120.
Calamoncosis laminiformis, 120.
Calamoncosis minima, 120.
calcipennis, *Microstigma* sp.n., 463.
Caliphaea confusa, 465.

Calliphora erythrocephala, 375.
Callyna, 250.
Callyna jugaria, 251.
Callyna monoleuca, 250.
Callyna siderea, 251.
Calogramma festiva, 245.
candezei, *Aulacoscelis*, 90.
capilliformis, *Protosticta*, 459.
 CARABIDAE, 394.
Carea subtilis, 249.
cariciphila, *Oscinella*, 141.
carnitorus, *Dermestes*, 484.
Carpophagus banksiae, 101.
Carpophagus excavatus, 101.
Carrot fly, immature stages, 355.
 CASSIDINAE, 475.
casta, *Fumea*, 29.
castanea, *Erythrodiplox*, 470.
Catamerus, 490.
 CEPHIDAE, 386.
 CERAMBYCIDAE, 420, 422, 475, 476, 479, 488, 495.
 CERAMBYCINAE, 423.
Cerambyx, 436.
Cerura, 25.
Cerura vinula, 21.
 CETONINAE, 488.
Chaetopteryx villosa, 197.
Chalcosoma, 488.
Charagia, 12, 21.
Chasmina, 238.
Chimarra, 196.
chinensis, *Melaphis*, 405.
Chionaspis euphorbiae, 68.
Chionaspis globosus, 64.
Chionaspis nigerensis, 65.
Chionaspis substriata, 64.
Chlorita arenicola, 151.
Chlorita (*Eremochlorita*) *uvaroviana* sp.n., 150.
Chlorita uvaroviana azerbeidzhanica subsp.n., 151.
Choristostialis enigmata, 398.
Chrysocorys, 14.
 CHRYSOMELIDAE, 75, 395, 474.
Chrysomphalus phenax, 62.
Chrysomphalus (*Pseudischinaspis*) *corticosus*, 62.
Chunrocerus gen.n., 155.
Chunrocerus balcanicus, 155.
Cicada reticulata, 43.
Cirphis unipuncta, 240.
c-nigrum, *Agrotis*, 242.
 COCCIDAE, 402.
 COCCINELLIDAE, 474.
cognata, *Oscinis*, 128.
Coloborrhis, 43.
coloratus, *Anthrenus*, 485.
confusa, *Caliphaea*, 465.
Conioscinella frontella, 129.
Conioscinella gallarum, 128.
Conioscinella halophila, 128.
Conioscinella mimula sp.n., 129.
Conioscinella sordidella, 129.
connata, *Erythrodiplox*, 471.
consanguis, *Polia*, 242.
Coolgardica, 97.
cophysa, *Tramea*, 223.
 COPRINAE, 488.
Coptotomus, 386.
Cordia myxa, 243.
 CORDULEGASTERIDAE, 466.

CORDULIDAE, 466, 472.
coriarius, *Prionus*, 419-442.
 CORYLOPHIDAE, 474.
 CORYDALIDAE, 394.
Corydalis, larva, 384.
Coryphaeschna adnexa, 467.
 COSSIDAE, 25.
Cossus cossus, 6.
cossus, *Cossus*, 6.
 CUCUJIDAE, 495.
Cucujopsis gen.n., 91.
Cucujopsis setifer sp.n., 91.
cultriformis, *Orthemis*, 467.
cuprea, *Argia*, 445, 447.
 CURCULIONIDAE, 398.
curtipenne, *Aphanotrigonum griseum*, 126.

D

Dacnonypha suborder n., 4.
Dadica lineosa, 246.
dagnina, *Argia*, 453.
damicornis, *Stenodontes*, 488.
Danaus plexippus, 337.
Danaus plexippus, seasonal variation in sex proportion and wing length, 337.
Darthula hardwickii, 39.
Dasythemis esmeralda, 468.
Dentaspis rugosa sp.n., 62.
Dentaspis substriata, 64.
Dermestes, 477, 478, 479, 480, 481, 482, 483, 493, 494.
Dermestes ater, 484.
Dermestes carnivorus, 484.
Dermestes lardarius, 484.
Dermestes maculatus, 484, 491, 493, 494.
Dermestes peruvianus, 484.
 DERMESTIDAE, 475, 476, 477, 479, 480, 482, 486, 492.
 DERMESTINAE, 477, 479, 480, 484.
diastema, *Elachiptera*, 147.
Dicraeus fennicus, 131.
Dicraeus ingratus, 130.
Dicraeus napaeus sp.n., 133.
Dicraeus raptus, 130.
Dicraeus scibilis sp.n., 132.
Dicraeus styriacus, 134.
Dicraeus tibialis, 131.
Dicraeus vagans, 131.
Dicraeus vallis sp.n., 133.
Dicterias, 443.
dido, *Micrathyria*, 470.
didyma, *Micrathyria*, 221.
difficilis, *Argia*, 220, 228.
Dineutes, 386.
Dinocampus rutilis, 388.
Dipterygia indica, 245.
Discogastrella germanica, 128.
dispacea, *Heliothis*, 24.
Ditrysia, 4.
ditzleri, *Triacanthagyna*, 467.
Drosophila confusa, 362.
Dryodurgades subgen.n., 158.
 DRYOPIDAE, 475, 476, 479, 486, 487, 492, 495.
Dryops auriculatus, 486.
Dryops ernesti, 487.
Dryops luridus, 486, 487.
Duboulaia, 97.
Duboulaia rugosa, 97.

Duplachionaspis ugandae sp.n., 64.
Dynastes, 488, 495.
Dynastes gideon, 488, 494.
 DYNASTINAE, 488, 492.
Dythemis fugax, 234.
Dythemis rufinervis, 234.
Dythemis sterilis, 222, 232.
Dythemis velox, 234.
 DYTISCIDAE, 395.

E

Ehretia laevis, 243.
Elachiptera diastema sp.n., 147.
Elachiptera, key to British species, 146.
elongallis, *Meitanaphis* sp.n., 406, 410, 411.
elongata, *Aulacoscelis*, 88.
elutella, *Ephestia*, 253, 299.
Elydna reclusa, 246.
Elydna transversa, 238.
Endoistatus, 43.
Enoicyla pusilla, 190.
ensigallis, *Macrorhinarium* sp.n., 406, 415.
Eohardyia subgen.n., 165, 171.
Epermenia, 14.
Ephestia elutella, breeding on bulk grain, 299.
Ephestia elutella, study of a population living on bulk grain, 253.
Ephestia kühniella, 276.
ephippiger, *Protosticta*, 459.
Epigomphus, 471.
Eremochloria subgen.n., 150.
Ergates, 488.
Ergates faber, 488.
Ergates spiculatus, 488.
Eribolus gracilior, 135.
Eribolus hungaricus, 135.
Eribolus nana, 135.
Eribolus slesviensis, 135.
Eriocrania, 6, 10.
Eriopus placodoides, 245.
 ERIOCRANIDAE, 2.
 ERIOSOMATINAE, 405.
ernesti, *Dryops*, 487.
Erythemis haematogastra, 471.
Erythemis plebeja, 222.
Erythrodiplax amazonica melanica, 470.
Erythrodiplax attenuata, 470.
Erythrodiplax basalis basalis, 470.
Erythrodiplax castanea, 470.
Erythrodiplax connata, 471.
Erythrodiplax connata fusca, 222, 470.
Erythrodiplax connata ines, 471.
Erythrodiplax kimminsi, 470.
Erythrodiplax ochracea ochracea, 222, 470.
Erythrodiplax umbata, 221.
Erythrodiplax unimaculata, 470.
esmeralda, *Dasythemis*, 468.
Eubria, 495.
 EUCOILIDAE, 388.
euphorbia, *Argia extranea* subsp.n., 457.
Euproctis, 25.
Eurymela, 43.
 EURYMELIDAE, 49. List of Genera, 51.
 EURYMELINAE, 49.
 EUSCELIDAE, 174.
Eusemia adulatrix, 251.
 EUSTHENIIDAE, 401.
Euzoa intracta, 247.
Euzoa spinifera, 247.

EUKNOIAE, 237.

- exigua*, *Laphygma*, 247.
exigua, *Oscinella* *frit*, 144.
expansa, *Zygynidia*, 153.
extranea, *Agrion*, 457.
extranea, *Argia extranea*, 456.
extraneum, *Agrion*, 457.
exustum, *Microstigma rotundatum*, 462.

F

- faber*, *Ergates*, 488.
fastigiata, *Uracis*, 468, 469.
femoralis, *Lioscinella*, 145.
femorata, *Aulacoscelis*, 88.
femorella, *Aphanotrigonum*, 126.
ferruginea, *Orthemis*, 221, 467.
festiva, *Calogramma*, 245.
FIGHTIDAE, 388.
flammeum, *Aelagrion*, 458.
flavescens, *Pantala*, 223.
Floraphis *gen.n.*, 406, 416.
Floraphis meitanensis *sp.n.*, 406, 416.
forficula, *Argia extranea* *subsp.n.*, 456.
frequentula, *Argia*, 543.
frontella, *Conioscinella*, 129.
Fruticoidia *subgen.n.*, 152.
fugax, *Dythemis*, 234.
fuliginosum, *Allothrombium*, 493.
fulvipes, *Aulacoscelis*, 90.
Fumea casta, 29.
fusca, *Erythrodiplax connata*, 222, 470.
fuscus, *Anthrenus*, 485.

G

- gallarum*, *Conioscinella*, 128.
GALLERINAE, 20.
Gampsocera inornata, 147.
Gangara thyrsis, 475.
gaumeri, *Argia*, 453.
GEOMETRIDAE, 12.
georgii, *Mesagallia*, 159.
germanica, *Oscinis*, 128.
gideon, *Dynastes*, 488, 494.
gigantula, *Staurophlebia*, 467.
gliricidae, *Melanaspis*, 60.
gloriosae, *Attagenus*, 484.
gloriosae, *Polytla*, 243.
Gnathocerus, 490.
Gnorimoschema, 12.
Goëra pilosa, 198.
GOMPHIDAE, 466, 467, 471.
Gomphoides, 471.
Goniopsita (Lasiambly) baliola *sp.n.*, 123.
Goniopsita palposa, 122.
Goniopsita parcepilosa *sp.n.*, 122.
gracilis, *Gynacantha*, 467.
grandis, *Aulacoscelis*, 88.
griseum, *Aphanotrigonum*, 126.
Gynacantha auricularis, 467.
Gynacantha gracilis, 467.
Gynacantha klegesii, 467.
Gynacantha litoralis, 467.
Gynacantha membranalis, 467.
Gynacantha nervosa, 220, 467.
Gynacantha tenuis, 467.
Gypona, 43.
GYRINIDAE, 395.

H

- Hadena oleracea*, 29.
HADENINAE, 237.
haematogastra, *Erythemis*, 471.
halophila, *Conioscinella*, 128.
hamulata, *Argia*, *sp.n.*, 447.
Hapleginella laevifrons, 145.
hardwickii, *Darthula*, 39.
hardwickii, *Urophora*, 43.
Hardya, 165.
Hardya anatolica *sp.n.*, 168.
Hardya (Eohardya) byzantina *sp.n.*, 173.
Hardya (Eohardya) mira *sp.n.*, 173.
Hardya iranica *sp.n.*, 166.
Hardya (Mimohardya) heptneri *sp.n.*, 170.
Hardya sevanensis *sp.n.*, 169.
Hardya turanica *sp.n.*, 167.
hargreavesi, *Scleromytilus*, 71.
hawswelli, *Mecistogaster*, 462.
Hectarthrurum, 495.
Helichus substriatus, 486.
Heliogaris, 443.
Heliogaris libera, 443.
HELIOTHINAE, 237.
Heliothis armigera, 24.
Heliothis dispasea, 24.
Heliothis scutosa, 24.
HELIOZELIDAE, 14.
Hemicentrus, 43.
Hemydacne, 97.
HEPIALOIDAE, 4.
HEPIALIDAE, 2.
Hepialus humuli, 7.
heptneri, *Hardya (Memohardya)*, 170.
Heranodes hudsoni, 480.
herculea, *Libellula*, 467.
HESPERIDAE, 25.
Hetaerina americana, 225.
Hetaerina dominula titia, 225.
Hetaerina macropus, 219, 223.
Hetaerina moribunda, 225.
Heteragrion, 465.
Heteragrion aurantiacum, 466.
Heteroneura, 4.
hilleri, *Thaumaglossa*, 485.
hirtus, *Trinodus*, 485.
HISPINAE, 474.
hogeii, *Aulacoscelis*, 90.
Holocentropus, 192, 198, 202.
Homoeophlebia, 393.
Homoneura, 4.
Hornibius sulcifrons, 91.
hortensis, *Oscinella*, 142.
huallaga, *Argia*, *sp.n.*, 450.
hudsoni, *Heranodes*, 480.
humuli, *Hepialus*, 7.
HYDRAENINAE, 395.
HYDROPHILIDAE, 395.
Hydrophilus caraboides, 386.
HYDROPSYCHIDAE, 181.
HYLICIDAE, 43. List of Genera, 46.

I

- Ibalia*, 388.
IBALIIDAE, 388.
ibofushi, *Nurudea*, 410.
Idiocerus balcanicus, 154.
Idiocerus nivosparsus, 156.

Idionyx, 471.
imbula, *Uracis*, 468, 469.
 INCURVARIIDAE, 2, 4.
indica, *Dipterygia*, 245.
indistans, *Trachea*, 245.
inermis, *Aphanotrigonum*, 128.
ines, *Erythrodiplax connata*, 471.
infrequentula, *Argia*, 451.
infumata, *Mecistogaster linearis* var.n., 462.
infumata, *Uracis*, 468, 469.
 Insect larvae, evolution of, 381.
insularis, *Olethrius*, 488.
 IPOINAE, 49.
iranicola, *Hardya*, 166.
iranicus, *Stenomelopiellus*, 176.
Ischnura ramburi var. *credula*, 220.

J

jugaria, *Callyna*, 251.

K

kaimosi, *Megarhinus*, 184.
kenyae, *Phenacaspis*, 66.
kimminsi, *Erythrodiplax*, 470.
klegesi, *Gynacantha*, 467...
kokama, *Argia*, 456.

L

laevigata, *Micrathyria didyma*, 469.
 LAMINAE, 423, 488.
Laphygma exigua, 247.
lardarius, *Dermestes*, 484.
 LATERIDIIDAE, 474.
Lepidostoma hirtum, 198.
Lepthemis vesiculosa, 222, 471.
 LEPTOCERIDAE, 190.
Leptocerus alerrimus, 198.
 LEPTURINAE, 423.
lepturoides, *Neodiaphanops*, 100.
Leto, 12.
Libellula herculea, 467.
 LIBELLULIDAE, 466, 467, 471.
libera, *Heliocharis*, 443.
ligustri, *Sphinx*, 29.
 LIMNEBIINAE, 395.
 LIMNOPHILIDAE, 190.
Limnophilus flavicornis, 203.
Lindingaspis magnifica, 57.
Lindingaspis opimus, 57.
Lindingaspis penniseti sp.n., 55.
Lindingaspis rossi, 57.
Lindingaspis rossi var. *colae*, 57.
Lindingaspis rossi var. *ferrandii*, 57.
linearis, *Mecistogaster*, 462.
lineosa, *Dadica*, 246.
Lioscinella femoralis sp.n., 145.
Lioscinella, key to British species, 144.
Lipara lucens, 119.
Lipara rufitarsis, 120.
Lipara similis, 120.
 LITHOSIDAE, 17.
litoralis, *Gynacantha*, 467.
litura, *Prodenia*, 247.
lounsburyi, *Phenacaspis*, 70.

lunatum, *Microstigma rotundatum*, 462, 463.
luridus, *Dryops*, 486, 487.
lutescens, *Megarhinus*, 177, 181.
 LYMANTRIIDAE, 5, 24.
Lynecestis amphiz, 238, 243.
Lystra reticulata, 43.

M

macropus, *Hetaerina*, 219, 223.
Macrorhinarium gen.n., 406, 412.
Macrorhinarium ensigallii sp.n., 406, 415.
Macrorhinarium ovogallii sp.n., 406, 412, 413, 415.
Macrothemis pumila, 471.
Macrotoma, 488.
Macrotoma serripes, 488.
maculatus, *Dermestes*, 484, 491, 493, 494.
makoka, *Argia*, sp.n., 455.
Mallodon maxillosus, 488.
 MANTISPIDAE, 386.
marchali, *Mecistogaster*, 460.
Marginaspis gen.n., 58.
Marginaspis thevetiae sp.n., 58.
Maurilia iconica, 249.
maurilia, *Spodoptera*, 240.
maxillosus, *Mallodon*, 488.
Mecistogaster, 460.
Mecistogaster hawxwelli, 462.
Mecistogaster jocaste vicentius, 462.
Mecistogaster linearis, 462.
Mecistogaster linearis infumata var.n., 462.
Mecistogaster marchali, 460.
Mecistogaster modestus, 462.
Mecistogaster ornatus, 461.
Mecynodera balyi, 102.
Mecynodera coxalgica, 102.
Mecynodera wickhami, 102.
megalopus, *Megapodagrion*, 465.
Megamerus kingii, 97.
 MEGAPODAGRIONIDAE, 460, 463, 465.
Megapodagrion, 465.
Megapodagrion megalopus, 465.
Megapodagrion setigerum, 466.
Megaptilus, 393.
Megarhinus barbipes, 177, 179.
Megarhinus brevipalpis, 178.
Megarhinus kaimosi sp.n., 184.
Megarhinus, key to Ethiopian species, 185.
Megarhinus lutescens, 177, 181.
Megarhinus nairobiensis sp.n., 181.
Megarhinus phytophagus, 177.
Megatoma, 480.
Megatoma undata, 485.
megatomoides, *Trogoderma*, 485.
Megopis (*Dandamis*) *nigropunctatus*, 488.
Meitanaphis gen.n., 406, 410, 412.
Meitanaphis elongalis sp.n., 406, 410, 411.
meitanensis, *Floraphis*, sp.n., 406, 416.
Melanaspis gliricidae sp.n., 80.
melanica, *Erythrodiplax amazonica*, 470.
melanocera, *Aulacoscelis*, 90.
Melanochaeta capreolus, 147.
Melanotus rufipes, 437.
Melaphis, 405, 408, 410.
Melaphis chinensis, 405.
Melaphis peitan sp.n., 405, 408.
Melaphis rhois, 405.
 MELICIPLETRINAE, 237.

MELOIDAE, 390.

MELOLONTINAE, 488.

melyroides, *Aulacoscelis*, 89.

MEMBRACIDAE, 39.

membracioides, *Balala*, 48.*membranalis*, *Gynacantha*, 467.*Mesagallia* gen.n., 157.*Mesagallia georgii* sp.n., 159.*Meteorus dimidiatus*, 388.*Metoponia rubriceps*, 375.*Metopator pusillus*, 397.*Microthyria aequalis*, 221.*Microthyria dido*, 470.*Microthyria didyma didyma*, 221.*Microthyria didyma laevigata*, 469.*Microthyria ocellata dentiens*, 221.*Microbracon hebetor*, 278.

MICROPTERYGIDAE, 2.

Microstigma, 443.*Microstigma calcipennis* sp.n., 463.*Microstigma rotundatum*, 462, 463.*Microstigma rotundatum exustum*, 462.*Microstigma rotundatum lunatum*, 462, 463.*Mimogaurax niger*, 134.*Mimohardya subgen.n.*, 165, 170.*mimula*, *Contoscinnella*, 129.*minor*, *Molorchus*, 437.*mira*, *Hardya* (*Eohardya*), 173.*Misagra parana*, 471.*misuyaca*, *Argia*, sp.n., 453, 454, 455, 456.

MNESARCHAEIDAE, 3.

modestus, *Mecistogaster*, 462.*Molanna*, 202.

MOLANNIDAE, 190.

molitor, *Tenebrio*, L., 492, 493, 494.*mollusca*, *Argia*, sp.n., 454.*Molorchus minor*, 437.*monoleuca*, *Callyna*, 250.*Monotrysis*, 4.*moribunda*, *Hetaerina*, 225.*moschata*, *Aromia*, 429, 432, 437.*Musca domestica*, 375.*museorum*, *Anthrenus*, 485.*Mystacides azurea*, 202.*Mystacides nigra*, 190, 202.

N

nairobiensis, *Megarhinus*, 181.*napaeus*, *Dicaeus*, 133.*Nealydia*, 12.*neavei*, *Sagra*, 108.*Necrobia*, 493.*Necrobia rufipes*, 493, 494.*Nemeritis canescens*, 276.*Neocordulia batei*, 472.*Neodiaphanops*, 99.*Neodiaphanops froggatti*, 99.*Neodiaphanops lepturoides* sp.n., 100.*Neodiaphanops pachytoides*, 100.

NEPTICULIDAE, 2, 4.

nervosa, *Gynacantha*, 220, 467.*Neuraeschna producta*, 467.*Neurolestes*, 465.*Neuronia*, 193, 198.*Neuronia ruficrus*, 198.*nigropunctatus*, *Megopsis* (*Dandamis*), 488.

NOCTUIDAE, key to larvae group A II, 238.

NOCTUIDAE, key to larvae group A VI, 249.

NOTODONTIDAE, 17.

Nurudea, 405.*Nurudea ibofushi*, 410.*Nurudea* (*Nuredopsis*) *shiraii*, 405.*Nurudea* (*Nurudea*) *sinica* sp.n., 405, 409.*Nurudea* (*Nurudeopsis*) *rosea*, 405.

NYMPHALIDAE, 26, 28.

O

ocellata dentiens, *Microthyria*, 221.*ochracea*, *Erythrodiplax*, 222.*ochracea*, *Erythrodiplax ochracea*, 470.

Odonata of Tobago, B.W.I., list of species collected, 215.

Odontestra submarginalis, 243.

ODONTOCERIDAE, 190.

Odontocerum, 198.*oleracea*, *Hadena*, 29.*Olethrius*, 488.*Olethrius insularis*, 488.*Oncopera*, 12.

OPOSTIGIDAE, 14.

orichalcea, *Argia*, 220.*ornatus*, *Mecistogaster*, 461.

ORPHILINAE, 477.

Orsodacne atra, 93.*Orsodacne cerasi*, 93.*Orsodacne lineola*, 93.*Orsodacne splendida*, 93.*Orsodacne variabilis*, 93.*Orthemis biolleyi*, 467.*Orthemis cultiriformis*, 467.*Orthemis ferruginea*, 221, 467.*Orthetrum sabina*, 467, 471.*Oryctes*, 488, 494, 495.*Oryctes rhinoceros*, 494.*Oscinella albiseta*, 139.*Oscinella angularis* sp.n., 141.*Oscinella angustipennis*, 139.*Oscinella cariciphila* sp.n., 141.*Oscinella frit* var. *exigua* var.n., 144.*Oscinella hortensis* sp.n., 142.*Oscinella*, key to British species, 138.*Oscinella nitidissima*, 139.*Oscinella posticata*, 139.*Oscinella trochanterata* sp.n., 140.

OSCINELLINAE, Table of Genera, 117.

Oscinimorpha albiseta, 125.*Oscinimorpha arcuata*, 125.*Oscinimorpha minutissima*, 125.*Oscinimorpha sordidissima*, 125.*Oscinis cognata*, 128.*Oscinis germanica*, 128.*Oscinis vindicata*, 128.*Oscinis vitripennis*, 128.*Oscinisoma*, 128.*ovipositorix*, *Uracis*, 468.*ovogallis*, *Macrorrhinarium*, sp.n., 406, 412, 413, 415.*Ozyethira*, 196.

P

PALEOSTIDAE, 14.

PAMPHILIDAE, 386.

Pantala flavescens, 223.

PAPILIONIDAE, 25.

- parana*, *Misagria*, 471.
Parandra, 422.
parcepilosa, *Goniopista*, 122.
parva, *Zeugophora* (*Pedrillia*), 96.
peitan, *Melaphis*, sp.n., 405, 406.
pellio, *Attagenus*, 485.
penniseti, *Lindingaspis*, 55.
Pennisetum sp., 57.
Penthimia, 43.
Perigea spp., 243.
Perithemis thais, 468.
 PERMOPHILIDAE, 399.
peruvianus, *Dermestes*, 484.
peruviansis, *Protoneura*, sp.n., 459.
Phaenoserphus viator, 388.
Phassus, 21.
Phenacaspis bauhiniae sp.n., 65.
Phenacaspis kenya sp.n., 66.
Phenacaspis lounsburyi, 70.
Phenacaspis lounsburyi var. *ekebergiae*, 70.
Phenacaspis whitehilli sp.n., 68.
Philoganga, 444.
Philonthus, 386.
 PHILOPOTAMIDAE, 191.
Philopotamus montanus, 198.
Phlegethontius quinquemaculata, 339, 351.
Phryganea, 193.
Phryganea grandis, 190.
 PHRYGANEIDAE, 190.
Phytomyza aquifolii, 375.
phytophagus, *Megarhinus*, 177.
piceus, *Attagenus*, 484.
 PIERIDAE, 6, 12.
Pieris, 6.
Pieris brassicae, 29.
placodoides, *Eriopus*, 245.
plagiata, *Tiracola*, 250.
Platygaster herrickii, 389.
 PLATYGASTERIDAE, 389.
platyptera, *Tetrathemis*, 471.
 PLATYSTICTIDAE, 464.
plebeja, *Erythemis*, 222.
plexippus, *Danaus*, 337.
 POGONOSCOPINAE, 49.
Poliaspis, 68.
Polia consanguis, 242.
 POLYCENTROPIDAE, 191.
Polyodaspis ruficornis, 121.
Polyodaspis sulcicollis var. *anglicus* var.n., 121.
Polyoptilus asper sp.n., 98.
Polyoptilus costatus, 98.
Polyoptilus gracilis, 98.
Polyoptilus lacordairei, 98.
Polyoptilus pachytoides, 97.
Polyoptilus pascoei, 99.
Polyoptilus torridus, 98.
Polytela gloriosae, 243.
Porcorhinus, 43.
 PRIONINAE, 420, 422, 488, 491.
Prionus coriarius, 419-442.
Prodenia litura, 247.
 PRODOXIDAE, 14.
producta, *Neuraeschna*, 467.
prolixus, *Rhodnius*, 314.
Prossbole elongata, 46.
 PROSBOLIDAE, 46.
Protomerpe permiana, 398.
Protoneura peruviansis sp.n., 459.
Protoneura protostictoides sp.n., 458.
Protoneura sancta, 459.
Protoneura tenuissima, 460.
 Protosticta, 459.
Protosticta capilliformis, 459.
Protosticta ephippigera, 459.
protostictoides, *Protoneura*, sp.n., 458.
 PROTOTHEORIDAE, 14.
 PSEPHENIDAE, 495.
Pseudelydna rufiflava, 249.
Pseudoips bicolorana, 475.
 PSEUDOSTIGMATIDAE, 443, 460, 465.
Psila rosae, 355.
 PSYCHIDAE, 20.
 PSYCHOMYIDAE, 191.
 PTILLIDAE, 474.
Ptilodactyla, 485.
 PTILODACTYLIDAE, 475, 476, 485, 486, 492, 495.
Ptinus tectus, 270.
pulla, *Argia*, 453.
pumila, *Macrothemis*, 471.
punctatus, *Ametalloides*, 103.
punctipennis, *Adoretus*, 495.
purpurea, *Aulacoscelis*, 90.
Pycnocerus, 490.
 PYRALIDAE, 28.
- R
- ramburi* var. *credula*, *Ischnura*, 220.
reclusa, *Elydna*, 246.
reducta, *Uraxis*, sp.n., 468.
reticulata, *Lystra*, 43.
reticulata, *Staurophlebia*, 467.
reticulatum, *Aetalion*, 41.
Rhagiosoma madagascariense, 101.
Rhagiosoma obscurithorax, 101.
Rhagium, 437.
Rhagium bifasciatum, 437.
Rhagoletis pomonella, 375.
rhinoceros, *Oryctes*, 494.
Rhizopertha dominica, 301.
Rhodnius prolixus, 314.
rhois, *Melaphis*, 405.
Rhyacophila, 196, 202.
 RHYACOPHILIDAE, 191.
rosae, *Nurudea* (*Nurudeopsis*), 405.
rosae, *Psila*, 355.
rotundatum, *Microstigma*, 462, 463.
rufinervis, *Dythemis*, 234.
rufipes, *Melanotus*, 437.
rufipes, *Necrobia*, 493, 494.
rugosa, *Dentaspis*, 62.
 RUTELINAE, 495.
- S
- sabina*, *Orthetrum*, 467, 471.
Sagra, key to subgeneric divisions, 105.
Sagra nevei sp.n., 108.
 SAGRINAE, certain genera excluded, 76.
 SAGRINAE, key to genera and tribes, 78.
 SAGRINAE-ORSODACNINAE, definition of group, 76.
sancta, *Protoneura*, 449.
sanguinea, *Aulacoscelis*, 89.
Sasunaga tenebrosa, 246.
 SATURNIDAE, 24.
satyrus, *Triacanthagyna*, 467.
 SCARABAEIDAE, 475, 476, 479, 488, 495.

Scardia, 26.
Scardia boleti, 21.
schäfferi, *Attagenus*, 485.
scibilis, *Dicraeus*, 132.
Scleromytilus gen.n., 71.
Scleromytilus hargreavesi sp.n., 71.
scotica, *Tropidoscini*, 137.
scutosa, *Heliothis*, 24.
selene, *Argynnis*, 28.
Selenocephalus stenopterus, 161.
Selenocephalus stenopterus simavensis subsp.n., 162.
Selenocephalus uvarovi sp.n., 163.
 SERICOSTOMATIDAE, 190.
serripes, *Macrotoma*, 488.
setifer, *Cucujopsis*, 91.
setigerum, *Megapodagrion*, 466.
Selodes argentipunctella, 198.
sevanensis, *Hardya*, 169.
shirazi, *Nurudea* (*Nurudeopsis*), 405.
 SIALIDAE, 394.
Sialis, larva, 384.
sidera, *Callyna*, 251.
Sideridis gr., 242.
siemensii, *Uracis*, 468.
sigillatus, *Stenomotiellus*, 176.
simavensis, *Selenocephalus stenopterus*, 162.
sinica, *Nurudea* (*Nurudea*), sp.n., 405, 409.
Siphonella oscinina, 121.
Siphunculina aenea, 123.
 SIRICIDAE, 386.
sordidella, *Conioscinella*, 129.
Sphecia bembeciformis, 25.
 SPHINGIDAE, 5.
Sphinx ligustri, 29.
spiculatus, *Ergates*, 488.
Spodoptera mauritia, 240.
 STAPHYLINIDAE, 474.
Statiophlebia gigantula, 467.
Statiophlebia reticulata, 467.
Stenodontes damicornis, 488.
Stenomotiellus, 174.
Stenomotiellus angorensis sp.n., 176.
Stenomotiellus araxis sp.n., 176.
Stenomotiellus iranicus sp.n., 176.
Stenomotiellus sigillatus, 176.
Stenopterygia subcurva, 242.
sterilis, *Dythemis*, 222, 232.
 STRATIOMYIDAE, 482.
subcurva, *Stenopterygia*, 242.
submarginalis, *Odontestra*, 243.
substriatus, *Helichus*, 486.
sulcifrons, *Hornibius*, 91.
sylvicola, *Agriogomphus*, 467, 471.
Syneta, 93.

T

Tegenaria domestica, 276.
Tenebrio, 490, 492, 494.
Tenebrio molitor L., 492, 493, 494.
 TENEBRIONIDAE, 475, 491, 492, 495.
tenebrosa, *Sasunaga*, 246.
 TENTHREDINIDAE, 386.
tenuis, *Gynacantha*, 467.
tenuissima, *Protoneura*, 460.
terminatum, *Anomisma*, 463, 464.
Tetrathemis platyptera, 471.
thais, *Perithemis*, 468.

Thaumaglossa, 480, 482.
Thaumaglossa bimaculata, 482, 485.
Thaumaglossa hilleri, 485.
 THAUMETOPOEIDAE, 17, 23.
theophora, *Tinea*, 21.
thevetiae, *Marginaspis*, 58.
Tholymis, 469.
 THYLODRIINAE, 477.
thyrsis, *Gangara*, 475.
tibialis, *Aulacoscelis*, 88.
Tinaea theophora, 21.
 TINAEIDAE, 1.
 TINAENINAE, 20.
Tinea uterella, 28.
Tinea walsinghami, 28.
Tinodes waeneri, 198.
Tiracola plagiata, 250.
 TISCHERIDAE, 14.
titia, *Hetaerina dominula*, 225.
Trachea indistans, 245.
Trachysiphonella, 123.
Tramea cophysa, 223.
translata, *Argia*, 220, 226.
Triacanthagyna ditzleri, 467.
Triacanthagyna satyrus, 467.
Triacanthagyna bicolor, 198.
Tribolium, 490, 491.
 Trichoptera, larvae of British, 187.
 Trichopterous larvae, key to the families, 208.
Tricimba cincta, 130.
Tricimba cincta var. *apicalis*, 130.
Tricimba lineella, 130.
trifoliata, *Argia*, sp.n., 449.
Trinodes, 480, 482.
 TRINODINAE, 477, 480, 482, 484, 485.
Trinodes hirtus, 485.
trochanterata, *Oscinella*, 140.
Trogoderma, 480.
Trogoderma megatomoides, 485.
Trogoderma versicolor, 483, 485.
Tropidoscini albipalpis, 136.
Tropidoscini antennata sp.n., 136.
Tropidoscini kerteszi, 136.
Tropidoscini nigrifrons, 136.
Tropidoscini scotica sp.n., 137.
Tropidoscini zurcheri, 136.
turanica, *Hardya*, 167.
Typhlodromus tineivorus, 276.

U

umbata, *Erythrodiplax*, 221.
umbriaca, *Argia*, sp.n., 451.
undata, *Megatoma*, 485.
unimaculata, *Erythrodiplax*, 470.
unipuncta, *Cirphis*, 240.
Uracis, 468.
Uracis fastigiata, 468, 469.
Uracis imbuta, 468, 469.
Uracis infumata, 468, 469.
Uracis ovipositorix, 468.
Uracis reducta sp.n., 468.
Uracis siemensii, 468.
Urophora hardwickii, 43.
uterella, *Tinea*, 28.
uvarovi, *Selenocephalus*, 163.
uvaroviana, *Chlorita* (*Eremochlorita*), 150.

V.

vallaris, *Dicraeus*, 133.
variabilis, *Aulacoscelis*, 90.
variegata, *Argia*, 451.
velox, *Dythemis*, 234.
verbasci, *Anthrenus*, 485.
versicolor, *Trogoderma*, 483, 485.
versutus, *Adoretus*, 495.
vesiculosa, *Lepthemis*, 222, 471.
vicentius, *Mecistogaster jocaste*, 462.
vindicata, *Oscinis*, 128.
vinula, *Cerura*, 21.
vitripennis, *Oscinis*, 128.
vorax, *Anthrenus*, 482, 485.

W

walsinghami, *Tinea*, 28.
whitehilli, *Phenacaspis*, 68.

X

Xorides albitarsus, 437.
 XYELIDAE, 386.

Y

yu, *Sideridis*, 242.

Z

Zelotypia, 14.
Zenithoptera americana, 469.
Zeugophora, key to genus, 94.
Zeugophora (*Pedrillia*) *parva* sp.n., 96.
Zeuzera, 25.
Zyginidia, 152.
Zyginidia (*Arboridia*) *expansa* sp.n., 153.
Zyzomma, 469.

